Phylogeny, Ecology, and Taxonomic Revision of the Travertine Beetles

(Coleoptera: Lutrochidae)

By

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Phylogeny, Ecology, and Taxonomic Revision of the Travertine Beetles (Coleoptera: Lutrochidae)

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Abstract

The Lutrochidae is a small, poorly known group of aquatic beetles, endemic to the Western Hemisphere. The evolutionary history of the group has never been examined in a phylogenetic framework, and much of its diversity is undescribed. Here, I present the first phylogenetic study of the group and a revised classification, which better reflects the evolutionary relationships in light of an extensive review of museum material.

Bayesian and Maximum Likelihood phylogenetic analyses of three genes (16S, 28S, and COI) strongly supported a close relationship with Dryopidae, which is consistent with published literature. However, the placement of the dryopid *Ceradryops* spp. as sister to Lutrochidae renders Dryopidae paraphyletic.

These same molecular phylogenetic analyses of the group recovered distinct, well-supported clades within Lutrochidae, which are corroborated by morphology, distribution, and ecology. As a result, the taxonomy of the group is revised to reflect evolutionary relationships recovered in phylogenetic analyses, and the following genera are erected: *Andotrochus* **n. gen.**, from Andean South America; *Auritrochus* **n. gen**., from North and northern Central America; *Berotrochus* **n. gen.**, from the Greater Antilles; and *Saxitrochus* **n. gen.**, from Andean South America. The genus *Andotrochus* **n. gen.** includes the species *Andotrochus minutus* (Maier & Short, 2013) **n. comb.** The genus *Auritrochus* **n. gen**. includes the species *Auritrochus arizonicus* (Brown and Murvosh, 1970) **n. comb.**, *Auritrochus laticeps* (Casey, 1893) **n. comb**., and *Auritrochus luteus* (LeConte, 1852) **n. comb**. The genus *Berotrochus* **n. gen.** includes *Berotrochus geniculatus* (Chevrolat, 1864) **n. comb.** The genus *Saxitrochus* **n. gen.** includes *Saxitrochus meridaensis* (Maier and Short, 2013) **n. comb.** The composition of *Lutrochus* **sensu.**

n. is revised to include only species from South and southern Central America that have a close association with submerged woody debris.

Morphological phylogenetic analyses recovered a tree with similar topology to the molecular analyses. Most branches were poorly supported, and a thorough re-evaluation of homology statements and character selection is necessary, and inferences about the group based on morphology can not be using the data in its current state.

Examination of museum specimens revealed eight species, new to science: *Andotrochus cordobensis* **n. sp.** from Argentina; *Auritrochus brunneus* **n. sp.** from southern Mexico; *Auritrochus shepardi* **n. sp.** from Mexico; *Lutrochus barrae* **n. sp.** from Central America; *Lutrochus gimmeli* **n. sp.** from Ecuador; *Lutrochus guarani* **n. sp.** from Paraguay; *Lutrochus tocache* **n. sp.** from South America; and *Lutrochus torrens* **n. sp.** from Central America. These species are described and descriptions, illustrations, photographs of historical type specimens, diagnoses, distribution maps for all twenty-nine species, including previously described species, are provided. An illustrated key to species of Lutrochidae of the world is also presented. A catalogue of world Lutrochidae species is included, and lectotypes are designated for the following species: *Lutrochus montanus* Grouvelle, *Lutrochus pilula* Erichson, and *Lutrochus geniculatus* Chevrolat.

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Crystal Anne Maier

July 2016

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Following the recommendation of Article 8 of the International Code of Zoological Nomenclature, taxonomic acts in this work are disclaimed for nomenclatural purposes.

Dedication

This dissertation is dedicated to the memory of my paternal grandfather, Otto Maier (1915–1998), who inspired me to to study “cavers [käfers]” and always had a bug from the garden to share with me.

Acknowlegements

First and foremost, sincere thanks are extended to my advisor, Andrew Short, whose knowledge of the water beetles helped me to navigate this massive (polyphyletic) grouping, whose words of encouragement motivated me to finish my dissertation, and whose collecting efforts have yielded more new species of Lutrochidae than any other individual collector. I would also like to thank my graduate committee and the University of Kansas Department of Ecology and Evolutionary Biology, who provided me with support and guidance throughout my time as a student.

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I also appreciate the support and patience of the staff of the Insect Collection at the Field Museum, who somehow endured nearly two years of the side effects of my attempts of juggling a full time job and a dissertation. In particular, I acknowledge Bill Stanley, who took a chance on me and offered the job of a lifetime, even though I felt may not have been ready for it.

I must also thank the collection managers and museums who loaned specimens for this study, for serving as stewards of the natural history specimens that have provided the basis for this work and for so graciously allowing me access to these treasure troves of information. Additionally, this work could not have been completed without the pioneering efforts of collectors, who often went out of their way to collect in unusual habitats to find Lutrochidae.

Finally, I'd like to thank my family and friends for their enduring support, particularly the past and present members of the Short Lab at KU, as well as my parents, Tony and Gloria, and my sister, Katie, who have supported me through what initially started as a strange hobby, but grew into a career.

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Chapter 1: INTRODUCTION TO THE TRAVERTINE BEETLES (COLEOPTERA: LUTROCHIDAE).

The Lutrochidae, commonly known as travertine beetles, are a family of small, brown, aquatic beetles associated with lotic habitats throughout most of the Western Hemisphere, ranging from southern Canada to Argentina. Lutrochidae contains twenty-one described species in a single genus, *Lutrochus*, and much of the diversity in the family remains unexplored (Maier & Short 2013, 2014).

The majority of described species can be placed into two distinct, informal "species-groups", with both groups defined by a unique set of life history traits, habitat preferences, and morphological characters. The species groups are as follows: the northern *Lutrochus luteus*-group, and the southern *L. pilula*-group; additionally, there are three species that do not fit into either group: *Lutrochus geniculatus*, *Lutrochus meridaensis*, and *Lutrochus minutus*.

The northern *Lutrochus luteus*-group, which encompasses three described species and two undescribed species, is confined to North America and northern Central America, extending as far south as Guatemala and Belize (Fig. 18). These species are found in carbonate streams in limestone-rich areas, particularly where travertine is deposited. The larvae bore through the travertine and consume the periphyton, which grows on the benthos (Brown 1991, Green 1975). The adults are agile fliers and are found on water-splashed rocks and crevices in the same habitats as the larvae. They are small, lack a tibial groove for reception of the mesotarsi, have long, falciform mandibles, and have distinctive elytral pilosity composed of flattened, scale-like golden setae.

The more southern *Lutrochus pilula*-group is comprised of eleven named species and six undescribed species, ranging from Argentina to southern Mexico (Fig. 18). All members of this

group tend to be large, possess tomentose elytra, robust mandibles, and a groove on the mesotibiae for reception of the mesotarsi. The larvae are long-lived, and bore into submerged woody debris, consuming large quantities of xylem tissue of the rotting wood (Valente-Neto and Fonseca-Gessner 2011). The adults remain in the same habitat, retreating to crevices on the surface of partially or fully submerged coarse woody debris. The adults are presumably scrapers of the biofilm growing on the surface of these logs.

Lutrochus geniculatus is known from the islands of Cuba and Hispaniola (Fig. 18). The adults share several morphological traits with those of the *L. pilula*-group, but share the ecological trait of developing in travertine streams, as those of the *L. luteus*-group. Because of this, *L. geniculatus* is a key taxon for understanding the transition between wood-boring to travertine-boring lifestyles. The larval habits are unknown, though the few specimens that have been collected share several key characters with larvae from the *L. luteus*-group.

Lutrochus meridaensis is restricted to hygropetric habitats in Mérida State, Venezuela (Fig. 18) (Maier and Short 2013). It is morphologically distinct from all other lutrochid species and its habitat preferences are unique among the Lutrochidae, in that it is apparently not associated with boring habits of any kind. The larvae are unknown.

The *L. minutus*-group includes a single described species and one undescribed species from western South America (Fig. 18). It is known from throughout the area surrounding the Andean belt, though not necessarily at high elevations, from western Venezuela south to Bolivia and Argentina. These are most often collected at UV lights, though their habitat appears to be in waterlogged debris is streams, as there is a series of specimens collected from “trash” in the Rio Surutu, Bolivia (H. P. Brown, in. litt.).

Additionally, the aquatic lifestyle and unique habitat preferences of Lutrochidae make this family an ideal candidate for exploring evolutionary and environmental lines of research. The ecological change between travertine-association and a wood-boring lifestyle represents an unusual evolutionary transition with the potential for providing insights to the evolution of wood-boring habits throughout Byrrhoidea and in Coleoptera as a whole. However, taxonomic research on Lutrochidae is lacking and the phylogenetic relationships between the members of the family and others in the superfamily Byrrhoidea have been unexplored in a cladistic framework.

Lutrochids are members of the coleopteran superfamily Byrrhoidea, a relationship which has been strongly supported by both morphological and molecular data in a number of studies (Figs. 1–8) (Hunt et al. 2007, Lawrence et al. 2011, & McKenna et al. 2015). Their exactly placement within Byrrhoidea has remained in question, however, because morphological studies (Lawrence et al. 2011) have conflict with molecular phylogenetic analyses (McKenna et al. 2015), with morphological data placing them in a clade with Heteroceridae and Elmidae, and molecular studies placing them sister to Dryopidae. Additionally, the internal classification of the family has never been examined.

Additionally, the tendency of the travertine beetles to prefer clean headwater streams makes them potential candidates as bio-indicator species for evaluation of water quality and environmental health. The closely related family Elmidae is regularly used in aquatic monitoring programs (Sinclair 1964, Garcia-Criado and Fernandez-Alaez 1995, Corbi et al. 2013), though the lack of accessible tools for identification and the sheer number of undescribed taxa have left Lutrochidae ignored as indicator species.

This study aims to address these deficiencies in the knowledge of Lutrochidae and open up the group for further study on biogeography, water quality requirements, and evolutionary transitions. This will be achieved through two objectives: (1) to reconstruct the evolutionary history of the group by inferring both a species-level phylogeny of the Lutrochidae based on both adult and larval morphological characters and molecular data from three genes (COI, 16S, and 28S), and (2) to revise the classification of the family such that it accurately reflects its evolutionary history and to document the undescribed diversity in the group, while providing tools for identification.

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Chapter 2: PHYLOGENY AND EVOLUTION OF THE LUTROCHIDAE.

INTRODUCTION

The small byrrhoid family Lutrochidae has never been studied in a phylogenetic framework, and little is known about its evolutionary history. Consequently, the historical classification and taxonomy of the family poorly reflects biological and ecological data, as well as evolutionary relationships within the family. While Lutrochidae is poorly studied and ecologically diverse, several putative morphological characters support the likely monophyly of the group, including: (1) an expanded apical maxillary palpomere, (2) interfacetal setae, (3) two connate ventrites, (4) clavate antennae, and (5) ommatidia of the eucone type and not the exocone type (as in Limnichidae) (Lawrence et al. 1999). Endemic to the New World, all species in the family are semi- to fully aquatic and live in marginal habitats in freshwater streams and rivers. The family inhabits a wide variety of microhabitats, and there appears to be morphologically distinct groups of species across the Western Hemisphere (Fig. LUTMAP1).

While there have been no attemps to untangle the Lutrochidae family tree, there have been several molecular phylogentic studies examining the internal relationships within other closely related families in Byrrhoidea (Including Limnichidae, Dryopidae, Elmidae, and Heteroceridae).

Here, I employ a combination morphological and molecular phylogenetic methods to (1) place the family in a larger framework of the superfamily Byrrhoidea, (2) infer hypotheses of the evolution of Lutrochidae at the species level, and (3) revise the classification of the family to better reflect these phylogentic hypotheses.

Taxonomic placement of Lutrochidae

The Lutrochidae has always been placed firmly in the series Elaterformia by virtue of synapormorphies of the genitalic and prosternal structures. Many elateriforms exhibit aquatic or "semi-aquatic" lifestyles and thus are historically united based on these ecological affinites in the clade Dryopoidea. More recently, together with the terrestrial moss-inhabiting family Byrrhidae, they have been reffered too as the Byrrhoidea. The members and status of each these groups has changed with each new phylogenetic study, and only now we are beginning to understand the true structure of this branch of the beetle tree of life.

Within Elateriformia, however, its relationship with other families has been controversial and changed over time. The assemblage of species that currently comprise the Lutrochidae was initially considered part of the Parnidae (a junior synonym of Dryopidae). This assemblage was later moved to Limnichidae before finally being separated into their own family by Kasap and Crowson (1975).

Three studies have placed Lutrochidae within the Elateriform superfamily Byrrhoidea based on morphological data (Figs. 1–8). A crude phylogenetic dendrogram appearing in Kasap and Crowson (1975) placed Lutrochidae in "Higher Dryopoidea" based on adult internal anatomy (Fig. 1). A later phylogenetic study of the Byrrhoidea by Costa et al. (1999) placed Lutrochidae within a monophyletic Byrrhoidea, in a clade with Limnichidae, Dryopidae, and Heteroceridae (Fig. 3). Lawrence et al. (2011), in a phylogenetic study of all Coleoptera using adult and larval anatomy, found Lutrochidae to fall into a paraphyletic Byrrhoidea+Buprestoidea, in a clade with Elmidae and Heteroceridae (Fig. 4). It is important to note that Byrrhoidea (*sensu* Lawrence and Newton 1995) was recovered as polyphyletic in Lawrence (2011), with the soft-bodied aquatic "Psephenoidea" coming out separately on the tree, suggesting that the

evolutionary history of this group is still not well understood (Fig. 4). Additionally, their ecologies are consistent with this relationship, since members of families in Byrrhoidea (such as Dryopidae, Elmidae, and Psephenidae) are among the few beetles that spend nearly their entire lives underwater.

Lutrochidae was not included in several recent molecular phylogenetic studies on Coleoptera evolution (Figs. 6–8). Lutrochidae was not included in a molecular phylogeny of Coleoptera conducted by Hunt et al. (2007), using 18S, 16S and COI (Fig. 6). Bocakova et al. (2007), using two nuclear and two mitochondrial genes, recovered Byrrhoidea (*sensu* Lawrence and Newton 1995) as paraphyletic, including Dascilloidea and Buprestidae nested in the Byrrhoidea clade (Fig. 5). Again, Lutrochidae was not included in this analysis. It does, however, support the monophyly of Dryopoidea, that is, those members of the previously defined Byrrhoidea that have an aquatic lifestyle.

Timmermans and Vogler, in their 2012 study of the mitochondrial genomes of aquatic Elateriformia ("Dryopoidea"), did not include many major lineages within "Dryopoidea", including Lutrochidae, though it is worth noting that "Byrrhoidea" sensu Lawrence and Newton was again shown to be paraphyletic, and includes closely related elateriforms in Dascilloidea (Fig.7). Dryopoidea, including all of the aquatic lineages of Byrrhoidea was recovered as monophyletic in a Bayesian analysis with strong support (Posterior Probability = 1.0). Additionally, they found a phylogenetically informative gene rearrangement with a $tRNA^{Pro}$–*nad6* translocation in Dryopoidea. It was unclear whether this marker was homologous in all groups of Dryopoidea, but represents a uniting character for the group, especially considering their aquatic affinities.

The most recent attempt to reconstruct the evolutionary history of Coleoptera (McKenna et al. 2015) included one representative of Lutrochidae (Fig. 8). In their analysis of data from eight nuclear genes, they found Byrrhoidea to be monophyletic (with weak support) and sister to either Buprestoidea (under Maximum Likelihood) or Elateroidea (Bayesian Analysis), with strong support. Interestingly, the group also included Podabrocephalidae, a family of uncertain placement, which has historically been associated with the cantharoid families of Elateroidea. Additionally, they estimated that Byrrhoidea emerged in the middle Jurrasic, ca. 160.03 mya (95% confidence interval:176.96 to 142.85 mya). Lutrochidae was sister to Dryopidae with strong support in both Maximum Likelihood (>95% bootstrap support) and Bayesian (Posterior Probability = 1.0) analyses. The Lutrochidae + Dryopidae clade also included Callirhipidae in the Bayesian analyses, but with weaker support (Posterior Probablilty =0.85). "Dryopoidea," in the historical sense, was found to be monophyletic with weak support in both the Maximum Likelihood and Bayesian analyses.

MATERIALS & METHODS

Taxon sampling and Outgroups

Twenty-four taxa within Lutrochidae from through its range and representing all species groups, were selected for phylogenetic analysis, including both described and undescribed species. Fifteen species were only available for morphological analysis. These species were represented by specimens that were too old to easily retrieve quality genetic material (e.g., >50 years old). The species *Lutrochus misellus* was omitted from analyses because the type series, the only specimens known to exist, could not be located. Thirteen taxa outgroup taxa were included in

morphological and molecular phylogenetic analyses, with emphasis placed on the taxa that have historically been placed near Lutrochidae in past analyses. Multiple examplars of Dryopidae were included as that family has been resolved as sister to Lutrochidae in prior analyses (Costa et al. 1999, Lawrence et al. 2011, McKenna et al. 2015). Trees were rooted with *Heterocerus* sp. (family Heteroceridae), a related family in Byrrhoidea.

Morphological Character Selection

Characters were selected based on observation of dissected specimens and review of past taxonomic literature. A list of characters, as well as definitions of character states are presented in Appendix 2. Most characters selected were those visible in a cleared and slide-mounted specimen, and a majority were taken from sclerotized external structures as this makes comparison with non-dissected taxa much easier. In addition, special attention was paid to characters of the genitalia and wing venation, as these characters have been shown vary between species (pers. obs.). Larval morphological character states and life history data was also included when known.

Morphological Phylogenetic Analysis

Specimens were disarticulated and examined for the morphological phylogenetic analysis (Specimens deposited in SEMC, unless otherwise noted). See Appendix III for a complete list of taxa. Those that are known from only one or two specimens were coded using only externally visible characters. The characters were coded in Winclada 1.00.08 (Nixon 2002). Characters were unweighted. Multistate characters were treated as unordered. Characters were polarized by outgroup comparison, under the assumption that the set of character states possessed by the

outgroup is the plesiomorphic state and the suite of character states possessed by the ingroup is the apomorphic state (Wiley and Liebermann 2011).

Parsimony analysis was performed using NONA (ver. 2.0) (Goloboff 1999) and TNT (Goloboff et al. 2003, Goloboff et al. 2008). In NONA, heuristic searches were performed using multiple tree bisection and reconnection (TBR) (hold: 1000; mult*n: 500; hold/: 10) and character state changes were mapped onto the tree using Winclada 1.00.08 (Nixon 2002). In TNT, "new technology" searches were conducted to find the shortest tree 1000 times. Bootstrap support values were calculated for all trees using TNT.

Tree searching under the Maximum Likelihood (ML) criterion was conducted in IQ-TREE (Nguyen et al. 2015, Minh et al. 2013), using the Mkv model of character evolution (Lewis 2001).

For both ML and parsimony analyses, clades supported by a bootstrap support value (BS) of >70 are considered strongly supported (Hillis & Bull 1993). Trees were exported and edited in FigTree ver. 1.4.2 (Rambaut 2014, http://tree.bio.ed.ac.uk/software/figtree/) and final figures were constructed in Adobe Illustrator.

Molecular Phylogenetic Analysis: Laboratory Methods

Most specimens used were collected directly into 100% ethanol and maintained at -80˚C. A few specimens gathered from other sources (museum material, loaned material) were stored in 70% to 95% Ethanol and stored at room temperature (~22˚C). In two instances, extractions were made from mounted museum specimens, in one instance (*Lutrochus geniculatus* from USNM), amplification was unsuccessful. Other included sequences were harvested from Genbank where noted. Phylogenetic methods ae summarized in figure 9.

Extraction. After specimens were selected for extraction, they were assigned an SLE (Short Lab Extraction) number and broken into two pieces between the prothoax and mesothorax. The tissues were lysed and DNA was extracted using a Qiagen DNeasy Blood and Tissue extraction kit. A modified version of the "Purification of Total DNA from Animal Tissues (Spin Column Protocol)" was used: samples were left to lyse in a 56˚C water bath overnight, and samples were eluted using a 50 µL wash two times, instead of a single 200 µL wash. Extracted DNA was kept at -20˚C.

Digested cuticle from the extractions was retained, dried, and card-mounted, along with all collection labels and voucher labels. These were retained as vouchers and deposited in the SEMC unless noted otherwise.

Targeted Gene Regions. Three gene fragments were selected for sequencing. Since past studies on the Byrrhoidea had success with 28S (~1000 bp) and 16S (~ 540 bp) rDNA, as well as the mitochondrial gene Cytochrome Oxidase I (COI; ~770 bp) genes, these three genes were selected for phylogenetic analysis of relationships within Lutrochidae and Byrrhoidea. King et al. (2011) used 28S to resolve species-level relationships within Heteroceridae and COI was used to reconstruct relationships within the laraine Elmidae (Čiampor et al. 2013, Čiampor et al. 2016).

Amplification and Purification. Fragments of COI, 16S, and 18S were amplified in single PCR reactions. All reactions were conducted in the Molecular Genetics Laboratory at the University of Kansas Biodiversity Institute.

Each PCR reaction used the following combination of reagents: 1.0 µL template DNA, 2.0 µL buffer solution, 1.0 µL 50 mM $MgCl_2$ buffer, 1.5 µL dNTP mixture (2.5 mM component concentration), 0.3 µL of each forward and reverse primers (10 µM concentration), 0.1 µL Invitrogen Platinum *Taq* Polymerase, and 13.8 µL sterile H_2O, for a total volume of 20 µL per

reaction. For 28S reactions, 0.5 μL of the promoter Dimethyl Sulfoxide (DMSO) was added to the mixture. Samples were placed in an MJ Research DYAD PTC-220 Thermal Cycler for amplification. Conditions for each gene are as follows: 28S – 98˚C for 4 minutes (hot start), then 98˚C denaturation for 30 seconds, followed by 51˚C annealing for 30 seconds, and 72˚C extension for 1 minute. This process was repeated 38 times, and followed by a final extension at 72˚C for 5 minutes. COI – 95˚C for 4 minutes (hot start), then 95˚C denaturation for 30 seconds, followed by 43˚C annealing for 30 seconds, followed by 72˚C extension for 1 minute. This process was repeated 36 times, and followed by a final extension at 72˚C for 5 minutes. Extractions had only a ~50% success rate with this protocol. 16S – 95˚C for 3 minutes (hot start), then 95˚C denaturation for 30 seconds, followed by 50˚C annealing for 30 seconds, and 72˚C extension for 1 minute. This process was repeated 34 times, and followed by a final extension at 72˚C for 5 minutes. Primers for each gene are outlined in Table 1, and include L81041R and MFL184 for 28S, Jerry and Pat for COI, and LR-J-12887 and LR-N-13395 for 16S.

Once PCR was complete, products were visualized using a gel electrophoresis rig with agarose gel, made with TAE buffer and stained with Gel Red (Huang et al. 2010). The agarose gel was viewed under UV light and checked for clean bands of PCR product. Amplified samples sent to Macrogen (Macrogen Inc., Seoul, South Korea, www.macrogenusa.com) were cleaned using a modified ExoSAP-it protocol. The mastermix for purification included 0.2uL of ExoSAP-it and 0.8uL dionized water for each sample. Samples were vortexed and placed in the thermocycler with the following program: 37˚C for 30 min, 80˚C for 15 min, 4˚C hold for ∞.

Molecular Phylogenetic Analysis: Sequencing and Alignment

Cleaned samples were sent for Sanger sequencing off-site at Macrogen (COI, 28S) and Beckman Coulter Genomics (16S) (Beckman Coulter Inc., Danvers, MA, www.beckmangenomics.com).

Sequences were cleaned and aligned using Geneious 9.1 for Windows. (http://www.geneious.com, Kearse et al., 2012). Sequences of all gene fragments were aligned using MUSCLE (Edgar 2004) with default settings in Geneious. Alignments were then edited by eye to ensure that there were no indels in the protein-coding gene (COI) and that alignments of variable-length fragments were free from any major inconsistencies or errors.

Alignment of the three gene fragments yielded 2,647 bp of data. Trees were constructed using data from 28S alone (1247 bp), 16S (556 bp), and 28S and 16S combined (1804 bp.) Final sequences will be deposited in GenBank and assigned GenBank accession numbers prior to publication.

Molecular Phylogenetic Analysis: Computational Methods

Preliminary trees were constructed within Geneious 9.1 to using the neighbor-joining algorithim with the default settings to check the alignment and note conflicts. The COI alignment was exported as a nexus file and imported into Mesquite 2.75 (Maddison & Maddison 2011, www.mesquiteproject.org) to check the alignment for stop codons and to check the reading frame of coding genes and ensure that the codon position begins with "1" and ends with "3." A Nexus file for each final alignment (28S alone; 16S alone; 28S and 16S combined; and COI, 28S, and 16S combined) was then exported from Geneious. In the cases where low branch supports were recovered in the three-gene trees, and because of the lack of sampling for COI,

single-gene trees for 28S, 16S, and a phylogenetic tree excluding COI were also constructed to check for incongruences between genes

To select the models of molecular evolution that best fits the datathe data for multiple gene alignments (28S and 16S combined and COI, 28S, and 16S combined) was run in PartitionFinder 1.1.1 (Lanfear et al. 2012) in Python 2.7 (Python Software Foundation. Python Language Reference, version 2.7. http://www.python.org). Models were searched from the MrBayes set of models of evolution using the greedy algorithmThe Substitution models for single genes were searched automatically in IQ-TREE as part of the Maximum Likelihood (ML) analysis.

Maximum Likelihood Analysis. The Maximum Likelihood analyses were run in IQ-TREE (Nguyen et al. 2015, Minh et al. 2013), using a Phylip alignment format and the partition scheme returned by PartitionFinder (only for the concatenated alignments, single gene analyses were set to auto-determine the best substitution model). IQ-TREE was set to use the default setttings for the Branch Support (Bootstrap) Analysis, with 1000 replicates, 1000 maximum iterations, and a 0.99 minimum correlation coefficient. No SH-aLRT branch test was run (not a default). Clades supported by a bootstrap support value (BS) of >70 are considered strongly supported (Hillis & Bull 1993). Trees were exported and edited in FigTree ver. 1.4.2 (Rambaut 2014, http://tree.bio.ed.ac.uk/software/figtree/) and final figures were constructed in Adobe Illustrator.

Bayesian Analysis. The Bayesian analyses were run in MrBayes 3.2.6 (Ronquist et al. 2012). The simplified nexus file, including a Bayes block, indicating partitions and settings, were uploaded to the CIPRES Science Gateway (Miller et al. 2010, www.phylo.org) and run remotely. Partitions for the concatenated alignments were set to the partitioning sceme returned by

PartitionFinder and single gene analyses used the substation models selected in the Maximum Likelihood analysis. Two independent, simultaneous analyses were run for each set of gene fragments. They consisted of eight Markov Chain Monte Carlo (MCMC) runs, including one cold and seven heated chains, running for 30 million generations. Convergence was indicated when the standard deviation (SD) of the split frequencies dropped below 0.05. If the runs converged, the default burn-in of 25% was deemed sufficient, and this was used to construct a 50% majority rule consensus tree. If the runs did not converge, a burn-in of 50% was selected, and checked again. Clades supported by a posterior probability (PP) of >0.95 are considered strongly supported (Erixon et al. 2003). Trees were exported and edited in FigTree ver. 1.4.2 (Rambaut 2014, http://tree.bio.ed.ac.uk/software/figtree/) and final figures were constructed in Adobe Illustrator.

Generic Concepts

While there are many formal concepts to define species (e.g., Wheeler and Meier 2000), the circumscription of higher-level taxa, particularly genera, is more subjective (Wiley and Leiberman 2011). Naming of new higher-level taxa is not to be taken lightly and in the case of named monophyletic clades, should only be done with sufficient evidence. In the context of this study, a genus must meet three qualifications: (1) it must be a monophyletic clade, supported by both morphological and molecular evidence; (2) it must be morphologically distinct, and easily diagnosable externally, and (3) the clade should, in general, be united by shared ecological traits, particularly those of microhabitat preference, distribution, and life cycle.

RESULTS

Model selection

For the three gene dataset, the partitions are as follows – 16S: GTR + I+ Γ; 28S: GTR + I + Γ; COI first codon position: SYM + I; COI second codon position: JC + Γ; and COI third codon position: HKY + Γ.

Morphological Analyses

Morphological analysis returned four most parsimonious trees. The strict consensus tree was well resolved, with only two documented polytomies at shallow nodes in the tree, though only four clades were recovered with strong bootstrap values (BS>50), with the exception of a clade with the limnichid genera Limnichidae n. gen. + *Byrrhinus* (BS=76), a clade with the dryopid genera *Sostea* + *Dryops* (BS=82), and a clade containing some representatives of *Lutrochus germari*.

The strict consensus tree shows a sister relationship between Dryopidae and Lutrochidae with poor support (BS<50), though Dryopidae was not monophyletic, with the genus *Ceradryops* returned in a clade containing all Limnichidae.

Lutrochidae appeared as a monophyletic clade on the tree with poor support (BS<50). Within Lutrochidae, the enigmatic species *Lutrochus meridaensis* was recovered as sister to the rest of Lutrochidae (except *Lutrochus maldonadoi*) with poor support (BS<50). The two other unusual Lutrochidae species, *Lutrochus minutus* and *Lutrochus geniculatus*, formed a clade sister to the *Lutrochus pilula*-group with low support.

The *Lutrochus luteus* species-group in Lutrochidae was recovered as monophyletic with low support (BS<50). Nearly all species in the *Lutrochus pilula*-group formed as a monophyletic clade with low support (BS<50), with the exception of *Lutrochus maldonadoi*, which was recovered as sister to the rest of Lutrochidae with poor support (BS<50).

Molecular Analyses

Maximum Likelihood and Bayesian Analyses both found nearly congruent tree topologies, with several strongly supported clades, particularly at deeper nodes (Fig. SIMPHY). Low branch supports were found on both Bayesian and Maximum Likelihood trees at some of the shallower branches, particularly between closely related species (Figs. 11 & 12).

Both Bayesian and Maximum Likelihood analyses recovered a well-supported monophyletic Lutrochidae (BS = 97/ PP = 1.0) (Fig. 10). A close relationship between Dryopidae and Lutrochidae (see McKenna et al. 2015) was found to be well supported in both analyses (93/0.98) (Fig. 10). However, the genus *Ceradryops*, an enigmatic southeast Asian genus of Dryopidae, is resolved as sister to Lutrochidae with strong support (95/0.99) (Fig. 10), rendering Dryopidae paraphyletic with respect to Lutrochidae. These relationships were also supported in the 16S and two-gene trees (Figs. 14 & BYR16S28SML). The presence of Lutrochidae in the this branch renders Dryopidae paraphyletic, because "Dryopidae" in the current sense does not include the Lutrochidae. While the topologies within Dryopidae were consistent between trees, with strong support for most internal nodes within Dryopidae, none of the nominal genera from South America were recovered as monophyletic (Figs. 11 & 12).

The enigmatic lutrochid species *Lutrochus meridaensis* and *Lutrochus minutus* showed less stability. *Lutrochus meridaensis* was consistently resolved as sister to the remaining

Lutrochidae, and this relationship is strongly supported in both Maximum Likelihood and Bayesian analysis (97/0.99) (Fig. 10). This relationship was also well supported in the 16S and two-gene trees (Figs. 14 & BYR16S28SML). In the 28S tree, *L. meridaensis* was recovered as sister to *L. minutus* in a clade sister to the *L. laticeps*-group with marginal support (BS=73) (Fig. 15). The relationship of *Lutrochus minutus* to other Lutrochidae is less clear and the topology varies between Bayesian and Maximum likelihood trees, with low support for a sister relationship with the Lutrochidae except *L. minutus* (PP=0.64) in Bayesian Inference, and marginal support for a sister relationship with the North American species groups (BS=71) in Maximum Likelihood analysis (Fig. 10).

The two largest clades within Lutrochidae, the *L. luteus*-group from North America (100/0.99) and the *L. pilula*-group from South America (100/0.99), were both strongly supported in the three-gene analyses (Figs. 11 & 12). These clades were also strongly supported in the 16S and two-gene trees (Figs. 14 & BYR16S28SML). In the 28S tree, the *L. luteus*-group was strongly supported (>95/>0.95), but the *L. pilula*-group was not (Fig. 15). This group was recovered as monophyletic in the 28S tree with only weak support (PP=55), and it excluded *L. "vestitus"* from Falcón state, Venezuela (Fig. 15).

Within the North American, *Lutrochus luteus*-group, very little divergence was found, with short branch lengths, and no clades supported except for a clade containing *Lutrochus luteus* and several undescribed Mexican species, split from *Lutrochus arizonicus* (>95/>0.95) (Figs. 11 & 12).

The *Lutrochus pilula*-group was well supported in all analyses (>95/>0.95). A clade including the Andean species *L. violaceus* and *L. montanus* was recovered with good support (88/0.96) (Figs. 11 & 12). Shallower relationships in the *L. pilula*-group were less well

supported, with boostrap support values below 70 for most nodes and posterior probabilities below 0.90. The exception is a clade containing *Lutrochus vestitus* from Belize and morphologically similar relatives from South America (recorded as *Lutrochus* "*vestitus*" on the tree), *Lutrochus acuminatus*, and *Lutrochus wao*, which had strong support values (92/0.95) (Fig. 16). The clade will be referred to as the *vestitus*-group in further discussions. This clade did not include all *L.* "*vestitus"* however.

The assemblage of specimens which were preliminarily identified as *Lutrochus vestitus* were not recovered as a monophyletic grouping, despite lack of putatative distinguishing morphological characters (Fig. 16). A branch of *L. "vestitus"* (Group 1) from across northern Venezuela was recovered with strong support (100/0.99), though its sister relationship with the *vestitus*-clade was not well supported (58/0.55) and not all *L. vestitus* from Northern Venezuela appeared in this branch.

Several well-estabished and morphologically distinct species were recovered in the *vestitus*-group, rendering it paraphyletic (Fig. 16). A specimen of *Lutrochus vestitus* that was from near the type locality (Belize) is nested in this branch, (Group 3) surrounded by *L. "vestitus"* and several named species, though there is weak support in both Bayesian and Maximum Likelihood analyses for its position. Indeed, it changes position from sister to the clade (*L. wao* + *L. "vestitus"* Group 5, Venezuela + *L. "vestitus"* Group 4) with low support (PP=0.34) in Bayesian Analysis to sister to the clade (*Lutrochus torrens* (MS name) + *Lutrochus acuminatus* + *L. "vestitus"* Group 2) in with good support (BS=92) in Maximum Likelihood analysis. *Lutrochus torrens* from Costa Rica was recovered as sister to a clade containing *Lutrochus acuminatus* + *L. "vestitus"* (Group 1) from the northwestern coastal region of Venezuela (Guárico and Aragua States) (Branch 2) with weak support (57/0.71). The

Venezuelan coastal *L. "vestitus"* (Branch 2) is strongly supported as sister to *Lutrochus acuminatus*.

DISCUSSION

Performance of molecular analyses

Both Maximum Likelihood and Bayesian analyses performed well for resolving deeper nodes, with all higher-level clades recovered with good support (Figs. 11 & 12). Topologies for the three-gene trees were broady concordant between both methods, with the exception a few shallow nodes. Individual gene trees, particularly 28S alone, yielded slightly differing topologies (Figs. 15 & 14). The topology of the three-gene tree was most similar with that of the 16S tree, indicating that 16S may have had the most influence in the combined analyses (Figs. 12 & 14). The set of taxa sampled for 16S was most complete of all of the genes. Removing COI had little effect on changing support or topology of the tree, other than minor changes to bootstrap support values.

Shallower nodes, particularly within the L. *luteus*-group of species, and the *L. pilula*-group, had relatively poor resolution and very short branch lengths (Figs. 11 & 12).

The addition of more taxa to the COI tree and addition of other rapidly evolving genes might provide more resolution for recently diverging lineages, though if no structure is recovered in these groups with the addition of more genes, then synonymy of the currently described species may be warranted.

Performance of morphological analyses

The strict consensus tree was well-resolved and largely congruent with the trees recovered in the molecular analyses, however consistently low bootstrap values across the entire tree prevent making well-supported inferences about the evolution of this group based on morphology alone (Fig. 17).

Regarding the topology of the tree, the placement of two taxa, in particular, suggest the spurious relationships in the analysis: *Ceradryops* sp. and *Lutrochus maldonadoi*. *Ceradryops*, a dryopid, is returned as sister to Limnichidae, a group to which it has no affinity in the molecular analyses (Fig. 17). This genus is highly derived morphologically, and this may be a result of a large degree of homoplasy in the genus. The placement of the morphologically distinct Venezuelan lutrochid *Lutrochus maldonadoi* may also be the result of a large degree of homoplasy as well (Fig. 17). This species possesses all of the necessary synapomorphies to place it in the *Lutrochus pilula*-group, however it also has additional autapomorphies that it does not share with any other species, as well as certain characters which appear to homoplasious, and presumably it is a highly derived *Lutrochus pilula*-group species. Unfortunately, the species is only known from a single series, collected in the 1950s. A reevaluation of homology statements is necessary, based on the unusual placement of these two species.

The low bootstrap values across the tree are indicative of larger issues with the morphological analysis. A bootstrap value is essentially a measure of the evidence for monophyly of a particular group in the phylogenetic tree. There are two main causes of low bootstrap supports, (1) low evidence for monophyly of a branch and (2) presence of a high level of homoplasy in the branch (Wiley and Leiberman 2011). In this case, the problem most likely lies in a high degree of homoplasy in the characters selected for analysis, as the presence of

strong putative synapomorphies in each group and evidence from molecular analysis support the monophyly of most groups recovered in the morphological analysis. A reevaluation of homology statements in a re-analysis is will likely improve bootstrap support values. Additionally, the inclusion of characters that are likely of greater importance evolutionarily, such as the structure of female and male genitalia and stucture of gut, will also likely improve performance.

Relationship between Dryopidae and Lutrochidae

The recovery of a clade inclusive of Dryopidae and Lutrochidae is consistent with recent hypotheses of the placement of Lutrochidae within Byrrhoidea (McKenna et al. 2015) (Figs. 11 & 12). This close relationship is also supported by several morphological characters, including the presence of interfacetal setae on the eyes, and the structure of the tegmen of the male genitalia, which is elongate, curved, and cylindrical, though the parameres are completely fused to the tegmen in North American species of *Lutrochus*.

The placement of a single genus of Dryopidae, *Ceradryops*, as sister to Lutrochidae is more surprising. *Ceradryops*, an enigmatic genus of Dryopidae from southeast Asia, was recovered as sister to the strictly New World Lutrochidae with good support in all analyses (Figs. 11 & 12). Morphologically, *Ceradryops* is unusual and highly derived among the Dryopidae, as it possesses a five to six segmented antennal club and a distinctive median setal patch on the apical abdominal ventrite (cf. Kodada and Boukal 2003).

The highly derived morphology of *Ceradryops* and its large geographical disjunction with Lutrochidae make it challenging to explain the highly supported sister relationship with Lutrochidae. *Ceradryops* lacks the synapomorphies that would place it in Lutrochidae, such as an expanded apical maxillary palpomere and 11-segmented antennae (Kodada and Boukal 2003).

The recent discovery of a *Ceradryops*-like lutrochid from Austral South America, though, does provide evidence to support this clade (Jäch pers. comm.). This relationship hints at a potential Gondwanan origin for the Lutrochidae, and a potential line of research to explore. Their shared affinity for hygropetric and marginal aquatic habitats also supports this relationship, as other Dryopidae are more typically found fully submerged in littoral and slow moving lotic habitats, or are completely terrestrial (Spangler and Staines 2001).

Given that *Ceradryops* renders Dryopidae paraphyletic (Fig. SIMPHY), changes to the family-level classification of Byrroidea may be warrented. One possible solution would be to fold Lutrochidae into Dryopidae, possibly affording it subfamily status. Coincidentally, this would reflect the original (*sensu* Erichson 1847 & *sensu* Grouvelle 1889) classification of *Lutrochus*. However, such a significant change to the taxonomy requires more evidence than is presented here. Taxon sampling among Dryopidae taxa was sparse, particularly among Old World and terrestrial taxa. A more thorough sampling of Dryopidae would further clarify and strengthen the relationship between these two families. In light of potential future studies on the phylogeny of Dryopidae, and given the limited data from within the family, no changes to the classification of Dryopidae or *Ceradryops* are made here.

Structure within the Lutrochidae and internal classification

The monophyly of Lutrochidae is well-supported in all analyses, and is consistent with morphological and ecological data (Figs. 10). Even morphologically distinct taxa, such as *Lutrochus minutus*, which were historically identified as an undescribed genus of Limnichidae, were recovered within Lutrochidae.

Several synapomorphies unite all Lutrochidae and distinguish them from other byrrhoid families: (1) expansion of the apical maxillary palpomere, though the degree to which it is expanded varies among species (Fig. 353); (2) loosely clavate 11-segmented antenna, with slightly thickened first and second antennomeres and a loose, nearly serrate club formed by the nine apical antennomeres (Fig. 354); (3) tarsi 5-segmented, short, compact (Fig. 349); and (4) metaventrite with excavations for reception of the legs (Fig. 348).

The monophyly of the family is supported by distributional and ecological data as well. Lutrochidae are only found in the Western Hemisphere, from Canada to Argentina (Fig. 18), and larvae are fully aquatic (in contrast with the terrestrial larvae of Dryopidae). The larvae of both of the largest clades of Lutrochidae have boring habits, and bore into either newly formed travertine or tufa (Fig. 140), or bore into submerged dead wood (Fig. 360). Adults of the family are also aquatic, though may be considered "semi-aquatic", as they are able to enter and exit the water readily and often live in specialized, marginal microhabitats in lotic habitats, such as seeps, water-splashed rocks, on waterfalls, or on water-splashed debris or wood.

The family displayed some distinct structure in phylogenetic analyses, and this has implications for the classification of the family, with the elevation of four new genera (Fig. 10).

Status of Lutrochus meridaensis. *Lutrochus meridaensis*, an enigmatic species known only from a single locality in the Venezuelan Andes, was only discovered recently in 2009. This species was recognized as unusual based on its hygropetric habits and its distinctive morphology. Its unusual position in the family is consistently confirmed by a well-supported sister relationship to the rest of Lutrochidae across all analyses (Fig. 10). Morphologically, it is unique among the Lutrochidae, as it bears a suite of characters which set apart from all other species, including: (1) completely bare metatibiae (Fig. 386); (2) entirely free parameres (i.e. not fused to

each other, nor to the tegmen) (Fig. 385); (3) expanded, but not truncate maxillary palps (Fig. 379); (4) a transverse row of elongate setae at the midline of the labrum (Fig. 377); (5) A bare patch on the metaventrite (376); and (6) the presence of distinct elytral puncure rows (372).

Given its distinct habitat preferences and morphology, and its clear position as sister to the rest of Lutrochidae, this species is transferred to its own, monotypic genus, *Saxitrochus* **n. gen.**

Status of Lutrochus minutus. The placement of another unusual species of Lutrochidae, *Lutrochus minutus*, is not entirely clear, though it is well-supported that the species does belong in Lutrochidae. The three-gene trees recover *L. minutus* as sister to Lutrochidae (excluding *L. meridaensis*), however, this relationship is not well supported, and there is inconsistency in the position of this species between the Maximum Likelihood and Bayesian analyses. Using Maximum Likelihood, the species is found to be sister to the *L. luteus*-group (Fig. 12), whereas in Bayesian Inference, a sister relationship with Lutrochidae (excluding *L. meridaensis*) was recovered (Fig. 11). There is notable incongruence among the different gene trees, with 16S indicating a sister relationship with the *Lutrochus pilula*-group with good support (BS = 90) (Fig. 14), and 28S returning it in a clade with the *L. luteus*-group + *L. meridaensis*, also with good support (BS = 92) (Fig. 15). The conflict between the two genes is likely the cause of its uncertain position. Morphology or biological data do not necessarily provide many insights in this case, as *L. minutus* is so distinctive and its biology is poorly known. Based on distribution, the relationship with *L. pilula*-group could potentially be sister to *Lutrochus minutus* (relationship proposed by 16S tree, BS = 90) (Fig. 14), and this would have some interesting implications for the evolution of xylophagy in the group. We know very little about the biology of *L. minutus*, but from field notes recorded by Harley Brown, *L. minutus* larvae and adults were

found in partially submerged water-splashed plant debris in a stream in Bolivia. This potentially sheds light on a transition from consuming wet plant debris to consuming larger woody debris in streams. Based on our understanding of Elateriformia evolution (McKenna et al. 2015, Timmermans 2012), this would represent an independent evolution event of xylophagy in the series.

Lutrochus minutus is morphologically distinct from all other species of *Lutrochus*, except for an undescribed species from Argentina. These two species share several synapomorphies, including: (1) completely setose metatibia (Fig. 72); 2) entirely free parameres (not fused to either the other paramere nor to the tegmen) (Fig. 73); 3) body pilosity long (Fig. 56); 4) elytra with coarse punctation (Fig. 59); and 5) the presence of four, waxy, setose pits on the first abdominal ventrite (Fig. 71).

The waxy pits of the first ventrite (Figs. 58 & 71) are unique among the Lutrochidae and they are uncommon across the rest of Byrrhoidea. *Ceradryops*, the unusual dryopid that is sister to Lutrochidae, also bears a similar pit on its abdomen, though it is on a different ventrite (center of the fifth ventrite). Given their differing positions and tree topologies, these structures are not homologous, though it is intriguing that this uncommon structure has asrisen twice on the same clade. The function of the pit is not known.

Given the distinct habitat preferences and morphology of *L. minutus* and its tentative position as an independent lineage within Lutrochidae, this species is transferred to its own, monotypic genus, *Andotrochus* **n. gen.**

Status of North American Lutrochus species (L. laticeps-group). The *Lutrochus laticeps*-group from North America was recovered as monophyletic (Fig. 10). This is consistent with morphological evidence as well as with the distribution of the group. This group is

restricted to North America, only making it as far south as Guatemala (Fig. 18). They also only live in carbonitic waters, or on "travertine," a character which is found nowhere else in Lutrochidae (Fig. 134–136). Several synapomorphies unite the group and distinguish it from all other Lutrochidae: (1) long, sickle-shaped mandibles (Fig. 110); (2) mesotibia without excavation for reception of the mesotarsus (Fig. 116); (3) Postcoxal lines of the metaventrite confluent with the katepisternal suture (Fig. 108); (4) tegmen completely fused to the parameres (Fig. 102); (5) distinctive golden luster; and (6) the wedge-shape of the body (Fig. 99).

Based the limited distribution and distinct morphology, as well as strong support for its status as an independent clade within Lutrochidae, the North American species, those in the *L. luteus*-group, are transferred to their own genus, *Auritrochus* **n. gen.**

At the species level, geographically disjunct and morphologically distinct "species" were found to have very short branch lengths and low support (Figs. 12 & 11). Only *Lutrochus arizonicus* appeared to be a clearly resolved species in the analyses. Perhaps most surprising was that specimens of *Lutrochus laticeps* from northern Oklahoma and south-central Kansas that were assumed to be separate species based on morphology and distribution, did not form a distinct clade, but were scattered throughout the *Auritrochus* clade. There is a strong possibility that these specimens may be *Lutrochus luteus* not *Lutrochus laticeps*, because the geographic delineation between *Lutrochus luteus* and *Lutrochus laticeps* is not clear, and these specimens are from close to the border between the two species' distributions. Though the results of the phylogeny may suggest that *Lutrochus laticeps* is a synonym of *Lutrochus luteus* no taxonomic changes are made at this time pending further study of these taxa. Addition of more specimens of *Lutrochus laticeps* from the eastern reaches of its range in the United States may help determine

where the line between the two species is drawn. Also, improving taxon sampling for faster-evolving genes, such as COI or adding other genes (e.g. CAD) may provide further resolution.

Status of southern Lutrochus species in the L. pilula-group. *Lutrochus* species in the *L.* "*pilula*-group" were recovered as strongly monophyletic in all analyses (Fig. 10). This is supported by geography (all species occur in Central and South America, south of the Yucatán Peninsula) (Fig. 18), ecology (all species are aquatic, larvae bore into coarse woody debris, and adults remain closely associated with the wood and are rapid fliers), and morphology. The following characters unite all species in the clade: (1) mandibles stout, with short incisors (352); 2) mesotibiae with excavation distally for reception of mesotarsi (Fig. 349); 3) parameres fused, but free from tegmen; 4) overall body shape and color (Fig. 357); 5) pilosity of erect golden to brown setae (Fig. 339); 6) postcoxal lines separate from katepisternal suture (Fig. 348). Thus, *Lutrochus* in the strictest sense has become much smaller as a result of this study, and only includes the species of *Lutrochus* with the aforementioned qualifications.

Within *Lutrochus* s. str., many nodes were poorly supported or had short branch lengths. Here, the most significant clades are discussed (Fig. 16).

At the base of *Lutrochus* s. str., the species *Lutrochus montanus* and *Lutrochus violaceus* are resolved as a well-supported branch (Fig. 16). This grouping is also supported by morphology, as these two species share similar genitalic structure - both have short, tubular, fused parameres (Figs. 300 & 344). They are also restricted to high mountain streams in South America, with *L. violaceus* endemic to the Merida Andes and *L. montanus* endemic to the Andes of Ecuador and Peru. This clade likely also includes an undescribed species from Panama and Costa Rica (*Lutrochus* "*barrae*" MS), which also possesses short, tube-shaped parameres and is restricted to higher elevation, mountainous areas.

***Lutrochus vestitus* and closely-related taxa.** The lower support values across the shallower nodes in Lutrochidae make it difficult to draw conclusions about species related to *L. vestitus.* Specimens that were initially identified as *Lutrochus vestitus* (*L. vestitus*-group) do not form a monophyletic group based on molecular data, though the specimens from different branches are not diagnosable externally (Fig. 16). A few branches were recovered with strong support.

Specimens in the *L. vestitus*-group can be identified by having a distinctive pattern of setation on the legs (Fig. 334), with apical protarsomeres that are nearly entirely setose, with only a small longitudinal glabrous patch ventrally, and a distinctive aedeagus (Fig. 332).

Even considering geography, there appears to be a lack of discernable geographic pattern within this clade. While specimens from certain sites, such as those from Falcón State, Venezuela, were all recovered on a single branch (Branch 5), specimens from other sites, such as SLE792 and SLE810, which were both from the same site in Barinas State, Venezuela, were recovered in separate clades, on distant branches (Branches 1 & 4), indicating within this *L. vestitus*-group that there may be both populations with narrow ranges and ones with wide geographic ranges (Fig. 16).

A potential solution to this problem would be to synonymize all species that appear in this clade with specimens of the *Lutrochus vestitus*-group. This would a plausible solution, if the clade only included taxa such as *Lutrochus wao*, which is only distinguished from *L. vestitus* by subtle differences in genitalia and setation of the legs. What is particularly surprising is that several morphologically distinct taxa, such as *Lutrochus* "*torrens*" MS and *Lutrochus acuminatus* are also contained within this clade, unusual, because support for the clade containing these species was statistically significant. *Lutrochus acuminatus* is so distinct, in fact,

that upon initial examination, I considered that *Lutrochus acuminatus* may be a distinct lineage, separate from other *Lutrochus*. It bears several characters which separate it from all other Lutrochidae, including expanded elytral epipleura (Fig. 171), distinctively compact tarsi (Fig. 183), and strongly-truncate apical maxillary palpomeres (Fig. 177).

In light of consideration of both molecular and morphological data, it would not be prudent to make any taxonomic changes to the species in the *Lutrochus* "*vestitus*" clade. Improving taxon sampling in Central America, closer to the type locality of the species (Guatemala), may resolve some of these issues (Fig. 16). The addition of more rapidly-evolving genes will also potentially improve the resolution and branch support of more recent divergences. Revisiting the morphology of the specimens from this clade, exploring structures such as female genitalia and the internal anatomy to find diagnostic characters may also help make sense of this enigmatic clade.

Status of *Lutrochus geniculatus* and brief discussion of biogeography. *Lutrochus geniculatus* from Cuba and Hispanola is the only species of *Lutrochus* known from the West Indies north of Grenada (Fig. 18). Unfortunately, it could not be included in the molecular analysis as extractions of genetic material from museum specimens (>50 years old) would not amplify for the selected genes using the protocols outlined here.

Based on morphological data, *Lutrochus geniculatus* is hypothesized to be sister to *Lutrochus minutus*, in a clade sister to South American *Lutrochus* s. str. species. This relationship is not well supported (BS<50) (Fig. 17). Its position as a close relative to *Lutrochus* s. str. does make sense in light of morphological data. It bears several synapomorphies which support this position, including: (1) apical excavation of the mesotibia (Fig. 162); (2) postcoxal lines of the metaventrite separate from the katepisternal suture (Fig. BERGN16); (3) setation

pattern of legs (Fig. 152); and (4) overall size, coloration, and shape are similar in both *Lutrochus* s. str. and *Lutrochus geniculatus* (Figs. 150 & 151). There are several characters which distinguish *Lutrochus geniculatus* from *Lutrochus* s. str., and these include its possession of: (1) blunt-tipped mandibles (Fig. 157); (2) parameres completely fused to the tegmen (Fig. 161); and (3) elongate, nearly filiform antennae (Fig. 155). Additionally, *Lutrochus geniculatus* is restricted to high-calcium streams (Fig. 166), as *Auritrochus* **n. gen.**, unlike *Lutrochus* s. str., which have broader habitat preferences, and *Lutrochus geniculatus* is only found in the Greater Antillies, where no *Lutrochus* s. str. have been found (Fig. 18).

Thus, *Lutrochus geniculatus* most likely represents an independent evolutionary lineage, sister to *Lutrochus* s. str. and restricted to the Greater Antilles. Based on habitat preferences and morphology, as well as its tentative position as an independent lineage within Lutrochidae, the species is transferred to its own, monotypic genus, *Berotrochus* **n. gen.**

The future addition of *Berotrochus* **n. gen.** samples can be used to explore questions regarding the biogeographic history of the family, particularly in regards to the divergence of the two major clades of Lutrochidae, as well as the colonization of the West Indies by lutrochids. Two events likely shaped the evolution of the lutrochid species – the formation and movement of the Cretaceous Island Arc ca. 80-70 mya (Iturralde-Vinent and McPhee 1999) and the breakup and subsequent reformation of the Panamanian land bridge roughly 3.5 mya (Stanley 1989).

Colonization of the West Indies via the CIA is well documented in freshwater fishes, including Cichlidae (Chakrabarty and Albert 2011, Chakrabarty 2006) and it is possible that lutrochids colonized the Greater Antillies via this same route.

Two species of Lutrochidae are present in the West Indies, *Berotrochus geniculatus* **n. comb.** in Cuba and Hispaniola, and *Lutrochus grenadensis*. It is highly likely that Lutrochidae

colonized the West Indies twice, once by *B. geniculatus* **n. comb.** and a second time more recently, by species from northwestern South America. Colonization of the West Indies by *Berotrochus geniculatus* **n. comb.** may have occurred via one of three routes: (1) from the south, via dispersal from the Lesser Antilles, in which case it would be more closely related to the northeastern South American species and *Lutrochus grenadensis*; (2) through a vicariance event, via the Cretaceous Island Arc, here it would be most closely related to the Western South American species, or (3) dispersal from the Yucatán, close to Belize – then it would be most closely related to the North and Central American species.

The first scenario is unlikely, as no Lutrochidae have ever been recorded from the West Indies between Grenada, which has faunistic affinities to continental South America, and Hispaniola, which has faunistic affinities with Central America. The Lutrochidae have apparently been very slow to colonize the West Indies from the south, as evidenced by their presence on Grenada, but no other Lesser Antillean islands. Therefore, it would have had to "hop" islands from the south and the Lutrochidae on the intermediate islands had to go extinct. Another possibility is that even with extensive collecting by coleopterists on the other islands, they simply have not been found. Additionally, this taxon is distinct from *Lutrochus* s. str. *Lutrochus* in that it lives on travertine.

This also further highlights the gap in the fossil record for Lutrochidae and Dryopidae, as calibration of the tree using fossils could potentially provide answers to these questions. The formation of the Panamanian land bridge led to the mixing of the faunas of North America and South America and is commonly known as the Great American Interchange (GAI) (Simpson 1950).

Addition of fossil taxa from Dryopidae or Lutrochidae could also help date the divergence between *Auritrochus* **n. gen**., which is confined to the Americas north of Honduras, and *Lutrochus* s. str., which is restricted to South and Central America north into Mexico. The family likely started as a single lineage, which was divided when the two continents split, evolved independently in their unique habitats and now co-occur in several sites in Central America. a result of the biogeographic split between North and South America and subsequent connection of North and South America by way of a Panamanian land bridge at 3.5 mya.

TAXONOMY

Andotrochus Maier & Short n. gen.

Type Species. *Andotrochus minutus* (Maier & Short, 2013) **n. comb.**

Included Species: This is a monotypic genus, with only one included species.

Diagnosis. *Andotrochus* **n. gen.** represents a unique body plan among Lutrochidae, with numerous characters setting it apart from the other South American lutrochids, including strongly punctate elytra (Fig. 59), pubescent mesotibiae (Fig. 72), and parameres that are not as fused as in other Lutrochid species (Fig. 73). Additionally, this genus lacks the excavations in the hypomeron and elytral epipleuron characteristic of other Lutrochidae (Fig. 58).

Description. Body length 2.4–2.6 mm; width 1.3–1.5 mm. Body ovate, dark brown to black, densely pubescent; clothed with short, fine, recumbent light golden setae and long, erect light golden setae (Fig. 56).

Head broadly rounded. Eye rounded, large, with short, golden interfacetal setae; eyes projecting slightly from outline of head (Fig. 62). Antenna short, reaching slightly past anterior border of pronotum, 11-segmented; antennomeres clothed with short golden setae (Fig. 68). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically. Apical margin of labrum straight, lacking apical setal brush. Labrum sub-rectangular, clothed with sparse, blunt setae at basal half, apical half with setae becoming sparse (Fig. 63). Mandibles large, dark brown, wedge-shaped (Fig. 64). Maxilla with 4-segmented palpus, apical palpomere flattened and weakly triangular, truncate at apex; apical palpomere with small sensilla medially (Fig. 65). Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, two times as wide as long at base, sinuate at base, densely clothed in recumbent setae in a wavy pattern and long, erect setae (Fig. 59); lateral edges strongly convergent; pronotum with basal sublateral carinae. Lateral edge of pronotum with distinct bead, explanate apically. Posterior margin of pronotum straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, about as wide as long (Fig. 66, 60); anterior border of scutellum slightly concave. Hypomeron not excavate posteriorly (Fig. 58), lacking oblique carina. Area lateral to scutellum with distinct space between elytron and pronotum (Fig.60).

Elytron pubescent, dark brown, widest at base. Elytron slightly convex, with dense, deep, confused punctation; clothed in dense recumbent setae in a wavy pattern, and long, erect setae (Fig. 59). Elytral humerus strongly protuberant. Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 58).

Prosternum transverse, approximately as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, pointed posteriorly (Fig. 57). Metaventrite pubescent, lacking glabrous patch

medially, with dispersed deep and strong punctures on disc (Fig. 67). Metaventrite with metafemoral lines broadly separated from the katepisternal suture, lacking distinct mesotarsal rests. Mesepisternum and mesepimeron continuous, not excavate to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae. Wing venation reduced. (Fig. 61).

Legs long and slender. Profemur densely pubescent. Protibia entirely pubescent. Protarsus with all tarsomeres pubescent, clothed with dense, golden setae; apical tarsomere as long as preceding four tarsomeres combined. Mesocoxa lacking tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia predominantly pubescent, lacking excavation for mesotarsi. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere almost as long as preceding four tarsomeres combined. Plate of metacoxa strongly excavate medially (Fig. 57). Metatrochanter globose, without posterior extensions (Fig. 70). Metafemur densely pubescent.

Abdomen densely pubescent, with five ventrites. First ventrite shallowly excavated for reception of folded hind legs (Fig. 71); metacoxal rests on first ventrite each with two deep, wax-filled pits (Fig. 71). Apical ventrite broadly rounded.

Aedeagus slender and curved, becoming more curved at tapered tip. Parameres only slightly fused, pointed, with distinct lobes interiorly subapically (Fig. 73).

Etymology. The generic name *Andotrochus* is derived from the Andes mountains, in reference to the mountainous habitats of this genus, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. This species is removed from *Lutrochus* and placed into a separate genus based on its distinctive morphology and putative ecological differences. Given their distinctive

habitus, which bears striking superficial resemblance to the Limnichidae, *Andotrochus* **n. gen.** has historically been misidentified. In fact, three water beetle specialists (CAM, Harley P. Brown, and Paul J. Spangler), on separate occasions, identified specimens of *A. minutus* as "Limnichidae new genus." It was not until the specimens were examined more closely, that the characters placing them in Lutrochidae were recognized.

It is known from throughout the area surrounding the Andean belt, though not necessarily at high elevations, from western Venezuela south to Bolivia and Argentina. These are often found at UV lights, though their habitat appears to be in waterlogged debris is streams, as there is a series of specimens collected from "trash" in the Rio Surutu, Bolivia (H. P. Brown, in. litt.).

Comparative Notes. Despite its deceptive superficial similarity to Limnichidae, the genus possesses the necessary synapomorphies which place it in Lutrochidae – expanded apical maxillary palpomeres (Fig. 65), short, clavate antennae (Fig. 68), and interfacetal setae (Fig. 62) all point clearly to its place in Lutrochidae.

***Auritrochus* Maier & Short n. gen.**

Type Species: *Auritrochus luteus* (LeConte, 1852) **n. comb.**

Included Species:

Auritrochus luteus (LeConte, 1852) **n. comb.**

Auritrochus arizonicus (Brown and Murvosh, 1970) **n. comb.**

Auritrochus laticeps (Casey, 1893) **n. comb.**

Diagnosis. This genus is distinct, but most closely resembles *Berotrochus* **n. gen.** in vestiture of legs, and possesses the following suite of characters which separate it from all other

genera: body form strongly wedge-shaped, with a distinctive golden sheen (Figs. 76 & 121); antennae short, reaching no further than half-way down pronotum (Figs. 100 & 122); head lacking two rugose patches at occiput; mandibles large and sickle-shaped; mesotibiae lacking excavation for reception of mesotarsi (Fig. 132); mesotibia completely glabrous (Figs. 125 & 123); parameres of male genitalia broadly joined to tegmen; tegmen elongate and strongly curved (Fig. 102). Specimens of *Auritrochus* **n. gen.**are also significantly smaller than members of *Lutrochus* and Berotrochus **n. gen.**, ranging in size from 3.0 mm to 4.9 mm in length.

Description. Body length 3.0–4.9 mm and body width 1.3–2.6 mm. Body strongly wedge-shaped, golden metallic to light brown in color, densely pubescent; completely clothed with setae (Fig. 99).

Head broadly rounded, deflexed ventrally, grooved beneath eye for reception of antenna. Eye rounded, with short golden interfacetal setae; eyes strongly projecting to smooth within outline of head. Antenna short, barely reaching anterior border of pronotum (Figs. 100 & 122), clothed with short, golden setae. Mouth strongly hypognathus. Frontoclypeal suture indistinct. Clypeal margin strongly curved, clothed with setae (Fig. 100). Labrum evenly clothed with recumbent setae, lacking transverse row of long setae at midline (Fig. 114). Mandible large, narrow, dark brown, sickle-shaped, often with only one broad, distinct tooth apically (Fig. 110). Maxilla with 4-segmented palpus, apical palpomere flattened and sub-cylindrical, greatly expanded at apex (Figs. 113). Labial palpus 3-segmented; apical palpomere sub-cylindrical, with field of sensillae at apex (Fig. 112).

Pronotum pubescent, weakly bisinuate at base (Fig. 99); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, not explanate to slightly explanate laterally at base (Fig. 101). Posterior margin straight or only shallowly excavate to

receive anterior margin of scutellum. Disc of pronotum convex (Fig. 101). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur (Fig. 101).

Elytron pubescent, brown to brownish-black, with distinct golden sheen, widest at base of elytron. Elytron strongly convex, strongly wedge-shaped, broadly rounded; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent or erect setae; humerus strongly protuberant (Figs. 99). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Figs. 100). Elytral apex rounded to acuminate.

Prosternum transverse, approximately twice as wide as long, deflexed or not deflexed to accommodate head; prosternal process acute or rounded posteriorly. Metaventrite entirely pubescent; metafemoral lines nearly confluent with katepisternal suture, with distinct mesotarsal rests (Fig. 108). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 101).

Legs long and slender. Profemur densely pubescent, protibia entirely pubescent (Fig. 107). Protarsus with at least first four tarsomeres tomentose, particularly ventrally; apical tarsomere with varying degrees of setation. Mesofemur densely pubescent. Mesotibia entirely glabrous, mesotibia smooth, not expanded, with apex smooth, lacking excavation for reception of mesotarsus (Fig. 116). Mesotarsus glabrous (Fig. 107). Metatrochanter excavate for reception of metatibia, with weak or no posterior projection (Fig. 100). Metafemur densely pubescent. Metatibia entirely tomentose, except for small bare patch at apex. Metatarsus with first four tarsomeres entirely tomentose; apical metatarsomere with varying degrees of setation (Figs. 107 & 82).

Abdomen entirely pubescent, with five ventrites, ventrites constricted medially (Fig. 77). Metacoxal rests on first ventrite extending half to two thirds of the way to second ventrite. First

ventrite excavated for reception of hind legs. Apical ventrite of male rounded to very shallowly notched (Fig. 77).

Male genitalia as illustrated, tegemen elongate, narrow, and strongly curved parameres pointed and broadly joined to basal piece (Fig. 102). Aedeagus strongly curved. Parameres nearly completely fused.

Comparative Notes. Morphologically, *Auritrochus* **n. gen.** bears many similarities with *Andotrochus* **n. gen.**, including its small size and metallic sheen. Interestingly, the ovipositors in both *Auritrochus* **n. gen.** and *Andotrochus* **n. gen.** are similar, with a blunt apex instead of a strongly sickle shaped apex, as in *Lutrochus*. The elongate and pointed apex in *Lutrochus* may be the result of an adaptation to ovipositing in waterlogged wood and need to be able to insert the eggs into the crevices in wood. Both *Auritrochus* **n. gen.** and *Andotrochus* **n. gen.** lack the apical excavation of the mesotibia.

Ecologically, *Auritrochus* **n. gen.** and *Berotrochus* **n. gen.** occupy similar niches in their ranges, with both genera preferring high-calcium travertine streams – *Auritrochus* **n. gen.** in North and Central America, and *Berotrochus* **n. gen.** in the Greater Antilles.

Biology and Distribution. The five species of *Auritrochus* are found throughout the northern part of the Western Hemisphere, from southern Canada to Belize – (with a dubious singleton from Costa Rica in OMNH collection).

Auritrochus **n. gen.** can be found in fast flowing rivers and streams in areas of high calcium (limestone & karst topography). Within these habitats, the adult beetles live on watersplashed rocks, detritus, and mosses, and they are almost never completely submerged. This genus can be locally abundant, with hundreds of adult beetles aggregating as the water's

edge in spring and summer. They are not well represented in collections, though, as this habitat is only rarely tapped for aquatic insect collections.

***Berotrochus* Maier & Short n. gen.**

Type Species *Berotrochus geniculatus* (Chevrolat, 1894) **n. comb.**

Included Species: This is a monotypic genus, with only one included species.

Diagnosis. This genus is distinct, distinguished from all other described Lutrochidae by the following combination of characters: body form nearly parallel-sided (Fig. 150); antennae reaching past half-way down pronotum (Fig. 150); head with two rugose patches at occiput; mesotibiae with excavation for reception of mesotarsi (Fig. 162); mesotibia of female with ventral tomentose strip; parameres of male genitalia immovably fused to tegmen (Fig. 161).

Redescription. Body length 3.0–4.9 mm and body width 1.3–2.6 mm. Body ovate, weakly parallel-sided, dark brown to black, densely pubescent; clothed with short fine, recumbent setae (Fig. 150).

Head broadly rounded, deflexed ventrally, weakly grooved beneath eye for reception of antenna. Eye rounded, small with short golden interfacetal setae; eyes slightly projecting from outline of head. Antenna long, reaching nearly halfway down length of pronotum (Fig. 150), clothed with short, golden setae. Mouth hypognathus. Frontoclypeal suture indistinct. Clypeal margin straight, evenly clothed with golden setae (Fig. 159). Labrum clothed with recumbent golden setae, lacking transverse row of long setae at midline (Fig. 159). Mandible large, dark brown, blunt, lacking distinct teeth (Fig. 157). Maxilla with 4-segmented palpus, apical

palpomere flattened and rounded-triangular, greatly expanded at apex (Fig. 156). Labial palpus 3-segmented; apical palpomere cylindrical, with field of sensillae at apex (Fig. 160).

Pronotum pubescent, roughly 2.1 times as wide as long at base, weakly bisinuate at base (Fig. 150); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, explanate laterally base (Fig. 151). Posterior margin only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum shallowly convex(Fig. 150). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur(Fig. 151).

Elytron pubescent, dark brown to black, widest in anterior quarter. Elytron shallowly convex, weakly parallel-sided; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent setae; humerus slightly protuberant (Fig. 150). Lateral edge with distict bead; epipleuron appearing narrow in ventral aspect. Elytral apex rounded to very slightly acuminate.

Prosternum transverse approximately twice as wide as long, explanate anteriorly to accommodate head; prosternal process sharply pointed. Metaventrite entirely pubescent; metafemoral lines extending nearly to the katepisternal suture, with distinct mesotarsal rests (Fig. 163). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 151).

Legs long and slender. Profemur densely pubescent, profemur entirely pubescent (Fig. 152). Protarsus with all tarsomeres tomentose. Mesofemur densely pubescent. Mesotibia entirely glabrous (in females with tomentose patch ventrally at apex), mesotibia smooth, not expanded, with apex excavated for reception of mesotarsus (Fig. 162). Mesotarsus glabrous (Fig. 152). Metatrochanter subrectangular (Fig. 161). Metafemur densely pubescent. Metatibia entirely

tomentose, except for small bare patch at apex.Metatarsus with first four tarsomeres tomentose, apical tarsomere glabrous in apical ¾ (Fig. 152).

Abdomen entirely pubescent, with five ventrites, ventrites not constricted medially (Fig. 164). Metacoxal rests on first ventrite extending two thirds of the way to second ventrite. First ventrite barely excavated for reception of hind legs. Apical ventrite of male shallowly notched(Fig. 164).

Male genitalia as illustrated, parameres blunt and immovably fused to basal piece (Fig. 153). Aedeagus broad, slightly curved.

Etymology. The generic name *Berotrochus* is derived from the Latin *Bero-* for "ocean nymph," referring to its distribution on the oceanic islands of Cuba and Hispaniola, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. The genus *Berotrochus* **n. gen.** is restricted to the Greater Antilles, and represents the only Lutrochidae in the northern part of the West Indies. This lineage is unique in that it shares many of its morphological features with *Lutrochus*, from the Southern Hemisphere, and it shares its habits of living in travertine-depositing streams with *Auritrochus* **n. gen.** in North America. Because of this, *B. geniculatus* **n. comb.** represents a key taxon for understanding the transition between wood-boring to travertine-boring lifestyles

Comparative Notes. Morphologically, *Berotrochus* **n. gen.** is most similar to the *Lutrochus* from Central and South America. It shares the following characters with that genus: mesotibia with excavation, dorsal surface covered in fine, golden setae, mandibles short, securiform. It differs, though, in significant ways, including the long antennae, vestiture of the female mesotibiae, the structure of the male genitalia, and its distinctive habitat preferences. *Berotrochus* **n. gen.** has two distinct rugose patches on the posterior face of the head, just

anterior to the occiput. It shares this distinct character with *Andotrochus* and it is not seen anywhere else in the Lutrochidae or Byrrhoidea.

***Lutrochus* Erichson, 1847**

Type Species: *Lutrochus pilula* Erichson, 1847

Included Species:

Lutrochus acuminatus Grouvelle, 1889

Lutrochus cauraensis Maier & Short, 2013

Lutrochus funkae Maier & Short, 2014

Lutrochus germari Grouvelle, 1889

Lutrochus gigas Hinton, 1939

Lutrochus grenadensis Maier & Short, 2014

Lutrochus gustafsoni Maier & Short, 2013

Lutrochus leeanneae Maier & Short, 2014

Lutrochus maldonadoi Maier & Short, 2013

Lutrochus misellus Grouvelle, 1896

Lutrochus montanus Grouvelle, 1896

Lutrochus vestitus-group (Sharp, 1882)

Lutrochus violaceus Maier & Short, 2013

Lutrochus wao Maier & Short, 2014

Diagnosis. This genus is distinct, but most closely resembles *Berotrochus* in size and vestiture of legs, and possesses the following suite of characters which separate it from all other genera: body form broadly ovate to slightly wedge-shaped (Figs. 170 & 329); antennae short,

reaching no further than half-way down pronotum (Figs. 265 & 313); head lacking two rugose patches at occiput; mesotibiae with excavation for reception of mesotarsi (Fig. 182); mesotibia of completely glabrous (Figs. 170 & 271); parameres of male genitalia broadly joined to tegmen (Fig. 186). Specimens of Lutrochus are also significantly larger than members of other genera, ranging in size from 4.0 mm to 6.6 mm.

Redescription. Body length 4.0–6.6 mm and body width 2.1–3.6 mm. Body ovate to wedge-shaped, reddish-brown to black, densely pubescent; completely clothed with setae (Fig. 304).

Head broadly rounded, deflexed ventrally, grooved beneath eye for reception of antenna. Eye rounded, with short golden interfacetal setae; eyes slightly projecting to smooth within outline of head. Antenna short to long, ranging from barely reaching anterior border of pronotum to reaching no further than half-way down pronotum (Figs. 265 & 313), clothed with short, golden setae. Mouth hypognathus. Frontoclypeal suture indistinct. Clypeal margin straight, clothed with setae (Fig. 351). Labrum evenly clothed with recumbent setae, lacking transverse row of long setae at midline (Fig. 351). Mandible large, stout, dark brown, falciform, with distinct teeth apically (Fig. 352). Maxilla with 4-segmented palpus, apical palpomere flattened and rounded to triangular, greatly expanded at apex (Figs. 353 & 289). Labial palpus 3-segmented; apical palpomere cylindrical, with field of sensillae at apex (Fig. 179).

Pronotum pubescent, weakly bisinuate at base (Fig. 170); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, not explanate to slightly explanate laterally at base (Fig. 171 & 362). Posterior margin straight or only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum convex (Fig. 267). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur (Fig. 267).

Elytron pubescent, reddish brown to black, widest in anterior half. Elytron shallowly to strongly convex, sometimes weakly parallel-sided, but most often broadly rounded; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent or erect setae; humerus not to weakly protuberant (Figs. 304 & 339). Lateral edge with distict bead; epipleuron appearing narrow to wide in ventral aspect (Figs. 267 & 172). Elytral apex rounded to acuminate.

Prosternum transverse, approximately twice as wide as long, deflexed or not deflexed to accommodate head; prosternal process acute or rounded posteriorly. Metaventrite entirely pubescent; metafemoral lines broadly separated from the katepisternal suture, with distinct mesotarsal rests (Fig. 345). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 267).

Legs long and slender. Profemur densely pubescent, protibia entirely pubescent (Fig. 274). Protarsus with at least first four tarsomeres tomentose, apical tarsomere with varying degrees of setation. Mesofemur densely pubescent. Mesotibia entirely glabrous, mesotibia smooth, expanded or not, with apex excavated for reception of mesotarsus (Fig. 182). Mesotarsus glabrous (Fig. 274). Metatrochanter excavate for reception of metatibia, with strong to weak posterior projection (Fig. 183). Metafemur densely pubescent. Metatibia entirely tomentose, except for small bare patch at apex.Metatarsus entirely glabrous to entirely tomentose (Figs. 274 & 296).

Abdomen entirely pubescent, with five ventrites, ventrites not or weakly constricted medially (Fig. & 344 & 287). Metacoxal rests on first ventrite extending half to two thirds of the way to second ventrite. First ventrite excavated for reception of hind legs. Apical ventrite of male rounded to very shallowly notched (Fig. 344).

Male genitalia as illustrated, parameres blunt and broadly joined to basal piece (Fig. 186). Aedeagus straight to slightly curved. Parameres nearly completely fused.

Comparative Notes. Morphologically, *Lutrochus* is most similar to the *Berotrochus* from the Greater Antillies. It shares the following characters with that genus: mesotibia with excavation, dorsal surface covered in fine, golden setae, mandibles short, stout, securiform. It differs, though, in significant ways, including the shorter antennae, vestiture of the female mesotibiae, the structure of the male genitalia, and its distinctive habitat preferences.

Biology and Distribution. The genus *Lutrochus* is restricted to Central and South America, from Southern Mexico (Los Tuxtlas, Veracruz, Mexico) to Northern Argentina (Cordoba, Cordoba, Argentina). While typical habitat for other genera are restricted to calcium-rich regions, specimens of *Lutrochus* have been collected from streams with a wide range of geologic characters (including high-calcium streams), from carbonitic and gneissic, to granitic geology.

Adults stay submerged and are covered in a thick coat of hydrofuge hairs. Adults and larvae are found on decaying wood and in crevices, while only larvae found in carved galleries in interior portions of the wood (Ide et al 2005). In the case of *Lutrochus vestitus*, may also be found in water-splashed plant debris and root mats (Maier & Short, 2013). Larvae are long lived and have a simple, straight gut, which leads to production of large quantities of feces – similar to other wood boring aquatic insects (Valente Neto and Fonseca-Gessner 2011).

The wood-boring habits of the *Lutrochus* s. str. are a unique and specialized life history. While a wood-boring lifestyle is common among terrestrial Coleoptera, it is an uncommon habit among aquatic Coleoptera. A small number of Ephemeroptera, Plecoptera, Coleoptera, Trichoptera, and Diptera species also utilize coarse woody debris in streams, though only a small

portion of these actually consume the wood. The majority of these species only use wood for shelter and/or as an anchor point in streams, or they scrape periphyton off the woody debris.

Besides *Lutrochus*, in Byrrhoidea several other species are known to inhabit coarse woody debris in streams. The western North American laraine *Lara avara* constructs galleries in hardwood logs in mountain streams (Dudley and Anderson 1982, Steedman and Anderson 1985). In Australia, elmids consume large quantities of submerged native *Eucalyptus* wood (McKie and Cranston 1998). The larvae of the enigmatic byrrhoid family Cneoglossidae, as well as those of several elmid species (*Macrelmis* sp. and *Stegoelmis* sp.) are found alongside *Lutrochus* larvae in Brazil (Costa et al. 1996, Valente-Neto and Fonseca-Gessner 2011).

***Saxitrochus* Maier & Short n. gen.**

Type Species: *Saxitrochus meridaensis* (Maier & Short, 2013) **n. comb.**

Included Species: This is a monotypic genus, with only one included species.

Diagnosis. This genus is distinct, and can be distinguished from all other described Lutrochidae by the unique diamond-shaped scutellum (Fig. 374), the glabrous hind tibiae (Fig. 386), the medial circular glabrous patch on the metaventrite (Fig. 380), and the presence of seven shallow rows of punctures on the elytron (369). *Saxitrochus* is also the only known genus in Lutrochidae to inhabit liverwort mats in hygropetric habitats (382).

Redescription. Body length 2.5–3.2 mm and body width 1.4–1.7 mm. Body strongly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with very short, fine, slightly recumbent golden hairs (Fig. 372).

Head broadly rounded, weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head (Fig. 375). Antenna short, reaching slightly past anterior border of pronotum, clothed with short golden setae (Fig. 375). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae nearly as long as labrum. Labrum clothed with sparse, blunt setae, with transverse row of long setae at midline. Mandible large, dark brown, stout, securiform. Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex (Fig. 379. Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, two times as wide as long at base, weakly bisinuate at base (Fig. 369); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, slightly explanate apically (Fig. 371). Posterior margin notched medially to receive pointed anterior margin of scutellum. Disc of pronotum broadly convex. Scutellum diamond-shaped, about as wide as long (Fig. 374). Hypomeron excavate posteriorly to accommodate femur (Fig. 371).

Elytron pubescent, dark brown, with slight metallic sheen, widest at base (Fig. 369). Elytron broadly convex, with seven rows of widely spaced coarse punctures (3 times diameter of punctures); intervals with dense setae; humerus not protuberant (Fig. 369). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 370). Elytral apex slightly acuminate.

Prosternum transverse approximately two times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acuminate posteriorly (Fig. 370). Metaventrite pubescent, with distinct, circular glabrous patch medially (Fig. 376); femoral lines extending nearly to the

katepisternal suture, with distinct mesotarsal rests. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender. Profemur densely pubescent. Protibia mostly pubescent. Protarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres. Mesocoxa with tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia curved slightly, completely glabrous, with small patch of golden setae at apex; mesotibia smooth, slightly expanded, apex without excavation laterally for reception of tarsus (Fig. 383). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, with single long seta (twice as long as preceding tarsomere) arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metatrochanter globose, without posterior extensions. Metafemur densely pubescent. Metatibia curved slightly, entirely glabrous, with small patch of golden setae at apex. Metatarsus glabrous, with apical tarsomere as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 370), ventrites constricted medially. Metacoxal rests of first ventrite extending nearly to second ventrite. First ventrite shallowly excavated for reception of folded hind legs. Apical ventrite of male broadly rounded.

Genitalia as illustrated, basal piece + parameres curved and short (relative to *Lutrochus* spp.) ca. 5x as wide as long. Aedeagus slender and very curved, becoming more curved at tapered tip (Fig. 385). Parameres only slightly fused, pointed, strongly tapering, with distinct lobes interiorly subapically.

Etymology. The generic name *Saxitrochus* is derived from the Latin *Saxi-* for "rock" or "stone", referring to its habitat on rock-face seeps, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. The species *Saxitrochus meridaensis* **n. comb.** is restricted to a single locality (Cascada Velo de la Novia "Bridal Veil Falls", Merida, Venezuela), but its unique habits and morphology, which are unlike any other species of Lutrochidae, warrant its transfer to an entirely new genus.

Comparative Notes. The genus *Saxitrochus* **n. gen.** most closely resembles the larger, more robust *Lutrochus*, and it is also distributed in South America like *Lutrochus*. However it possesses several distinct characters which are unique among the Lutrochidae – it is the only genus with both a glabrous mesotibia and glabrous metatibia. It also has a distinct glabrous patch medially on the metasternum and a diamond-shaped scutellum. *Saxitrochus* also lacks the mesotibial excavation, and has the abdominal ventrites constricted medially – characters it shares with the North American *Auritrochus* **n. gen.**

It does have the necessary characters which place it in Lutrochidae – expanded apical maxillary palpomeres (Fig. 379), short, clavate antennae (Fig. 381), and interfacetal setae (Fig. 375) all point clearly to its place in Lutrochidae.

KEY TO GENERA OF LUTROCHIDAE

1 Mesotibia with apical excavation for reception of tarsus (Figs. 182 & 284); West Indies and Central America to South America 2

- Mesotibia lacking apical excavation for reception of tarsus (Fig. 383); North America and Central America and South America along Andes 3

2(1) Body nearly parallel-sided (Fig. 150), mesotibia with small longitudinal patch of setae ventrally (Fig. 152), parameres of male genitalia nearly completely fused to the basal piece (Fig. 153); Greater Antilles ..... ***BEROTROCHUS* n. gen.**

- Body ovate, mesotibia completely glabrous, parameres of male genitalia not fused to basal piece; West Indies (Lesser Antilles) and Central to South America ..... ***LUTROCHUS* Erichson.**

3 (1) Metaventrite with medial circular glabrous patch (Fig. 376); scutellum diamond-shaped (Fig. 374); elytron with seven rows of shallow punctures (Fig. 369); apical maxillary palpomere narrow (Fig. 375); Mérida Andes, Venezuela ..... ***SAXITROCHUS* n. gen.**

- Metaventrite without medial circular glabrous patch (Fig. 67); scutellum triangular (Fig. 66); elytral punctation dense, confused, not in rows (Figs. 59 & 105); apical maxillary palpomere wide (Fig. 62) 4

4 (3) Body size small, less than 2.0 mm total length; body covered in long erect setae (Figs. 55 & 56); first abdominal ventrite with four pits (Fig. 71); South America .. ***ANDOTROCHUS* n. gen.**

- Body size larger, greater than 2.0 mm total length; body covered in golden, apressed, scale-like setae (Figs. 92 & 99); first abdominal ventrite smooth, lacking four wax-filled pits (Fig. 111); North America and Central America ..... ***AURITROCHUS* n. gen.**

CONCLUSIONS

This study has revealed some of the underlying structure within Lutrochidae and provided the taxonomic framework to pursue further study on the family. However, several improvements are necessary to make robust inferences about the evolution of this group.

The addition of key taxa to the molecular analysis is necessary in order to address certain conflicts in the data. First, broadening taxon sampling from Dryopidae, particularly those from the Old World, will help clarify hypotheses on the relationship between Lutrochidae and Dryopidae; second, increasing taxon sampling within Lutrochidae will address intra-familial relationships, specifically the addition of the West Indian species, *Berotrochus geniculatus*; and finally, inclusion of *Lutrochus* in the *L. vestitus*-group from Central America will potentially lead to greater resolution and understanding of this species-group.

More recent divergences and certain ambiguous branches may receive better support with the addition of two more genes. Plans to add CAD and to resolve amplification issue with COI could provide more resolution at these shallower nodes. Adding additional genes will also strengthen the previously recovered relationships.

Finally, the morphological analysis requires a thorough re-analysis. New knowledge obtained through molecular analyses and taxonomic revision will be used to inform homology statements and character selection. “Noisy” characters, which possess no phylogenetic signal, will be removed, and several newly-discovered characters will be added. Additionally, analyses will be run both with and without problematic taxa. A new and improved morphological data matrix will be added to the concatenated molecular matrix to produce a total evidence tree.

Once these issues are addressed, we can then use the data to explore new avenues of ecological and evolutionary research using the Lutrochidae.

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Chapter 3: TAXONOMIC REVISION OF THE LUTROCHIDAE

INTRODUCTION

The Lutrochidae or "travertine beetles" are a small aquatic family restricted to specialized lotic habitats throughout most of the Western Hemisphere. Currently, Lutrochidae contains twenty-one described species in published literature (Maier & Short 2013, 2014).

The aquatic lifestyle and unique habitat preferences of Lutrochidae make this family an ideal candidate for exploring evolutionary and environmental lines of research. The transition between travertine-association and a wood-boring lifestyle represents an unusual evolutionary transition with the potential for providing insights to the evolution of wood-boring habits throughout Byrrhoidea and in Coleoptera as a whole.

Additionally, the tendency of the travertine beetles to prefer clean headwater streams makes them potential candidates as bio-indicator species for evaluation of water quality and environmental health. The closely related family Elmidae is regularly used in aquatic monitoring programs (Sinclair 1964, Garcia-Criado and Fernandez-Alaez 1995, Corbi et al. 2013), though the lack of accessible tools for identification and the sheer number of undescribed taxa have left Lutrochidae ignored as indicator species.

Taxonomic History

This group has received little attention from systematists, with most published work being descriptive. Erichson described the type species, *Lutrochus pilula*, in 1847 from Brazil. He placed this species in Parnidae (=Dryopidae), in the tribe Dryopini, based on its long setation and

rounded body shape. LeConte (1852) was the first to record Lutrochidae from the Nearctic Region, describing the travertine beetle, *Lutrochus luteus*, from Texas. *Byrrhomorphus vestitus* was later described from Panama by Sharp (1882), though it was later moved to *Lutrochus*. Grouvelle (1889, 1896) then described four species from throughout South America and published the first key to species. Each of these early works provided only cursory identification information with few characteristics mentioned other than size and color. Subsequent species descriptions by Hinton (1939a) and Brown and Murvosh (1970) provided more detailed taxon accounts and included thorough morphological analyses and illustrations.

These species remained in Dryopidae until Hinton (1939a) transferred all described species of *Lutrochus* to the Limnichinae within Limnichidae, based on larval anatomy and the internal anatomy of the adults. Subsequently, Kasap and Crowson (1975) removed all *Lutrochus* species from Limnichidae and elevated the group to family status, without presenting explicit evidence for doing so. Brown (1987) supported this separation, citing major differences in larval morphology and ecological observations.

The currently described species are placed into five distinct genera: *Berotrochus*, from the Greater Antilles, northern *Auritrochus*, the *Saxitrochus*, from the Mérida Andes, *Andotrochus* from western montane South America, and the nominal genus *Lutrochus*, from the Americas south of Mexico (Fig. 18). A distinct suite of morphological characters and life history traits defines each genus, and the genera are well-supported in a phylogenetic context. Each individual genus prefers a distinct microhabitat, unique within the family.

Even with so few described taxa, species identification of travertine beetles has remained difficult. Early descriptions (e.g. Erichson 1847, LeConte 1852) are extremely generalized and could apply to hundreds of beetle species, many not even in Lutrochidae. The only published key

to species (Grouvelle 1896), utilized superficial characters such as body size and color. Additionally, many couplets refer to ambiguous characters or may apply to multiple species. Lack of taxonomic knowledge and an absence of reliable identification resources have left workers reluctant to identify species or describe new ones. Before a recent revision of the Lutrochidae of Venezuela (Maier & Short 2013), only two species, *Lutrochus germari* (Costa et al. 1996) and *Auritrochus arizonensis* (Brown and Murvosh 1980) received modern morphological treatments with detailed descriptions and illustrations. In recent years, there has been a period of significant growth for the family, with the number of described species nearly doubling after the publication of revisions of Lutrochidae of Venezuela and the Guianas. Many specimens in museum collections can still not be assigned to any currently described species and likely represent members of yet undescribed species (pers. obs.).

In total, there are twenty-one described species of lutrochids from the neotropics, though examination of material from throughout this region reveals that there are numerous undescribed species. The most recently described species from the neotropics were *Lutrochus gigas* Hinton (1939a) and several new species in Maier & Short (2013 & 2014), and only two modern works on life history of neotropical lutrochids have been subsequently published, both on the Brazilian species *L. germari* Grouvelle (Costa et al. 1996, Valente-Neto and Fonseca-Gessner 2011). Additionally, an identification barrier has existed, as Grouvelle's 1896 key, unfortunately, is lacking in detail and most of his descriptions and diagnoses can be applied to multiple lutrochid species.

These problems with establishing reliable identifications became apparent in the course of a revision of the family by the first author and was particularly obvious when the authors attempted to apply names to the more than 250 Lutrochidae specimens collected in a recent

survey of Venezuelan aquatic Coleoptera. In Venezuela, only a single species, *L. acuminatus* Grouvelle, was described prior to this work. We examined lutrochid specimens from several institutions in Venezuela and the United States and compared them with the types of several described species from northern South America. In this material, six undescribed species were identified from Venezuela alone, often only known from their type localities and to specialized habitats. This study resulted in the work "A Revision of the Lutrochidae of Venezuela" (Maier & Short 2013), and this study was the impetus for pursuing further study of the family through the examination of 2,450 specimens from biological collections around the world. Study of these specimens has revealed an additional nine species and has made evident the presence of two cryptic species complexes near *Lutrochus germari* and *Lutrochus vestitus*.

Here, all newly discovered species are described and detailed morphological descriptions, photographs, and illustrations for all new and currently described species are provided. Additionally, a traditional dichotomous key has been constructed to facilitate the further study of the systematics and biology of Lutrochidae.

MATERIALS & METHODS

Material Examined

For this study, 2,450 specimens were examined and are deposited in the following collections:

AMNH – American Museum of Natural History, New York, NY, USA (Lee Herman).

BYUC – Arthropod Collection, Monte L. Bean Life Science Museum, Provo, UT, USA (Shawn M. Clark).

BMNH – British Museum of Natural History, London, England (Maxwell Barclay).

CBBC – Cheryl B. Barr Collection, California, USA (Cheryl B. Barr).

CBDUG – Center for the Study of Biological Diversity, University of Guyana.

EMEC – Essig Museum of Natural History, Berkeley, CA, USA (Pete Oboyski).

FMNH – Field Museum of Natural History, Chicago, IL, USA (CAM).

FSCA – Florida State Collection of Arthropods, Gainesville, FL, USA (Paul Skelley).

INHS – Illinois Natural History Survey, Illinois, USA (Dmitri Dmitriev).

KBSC – Kansas Biological Survey Collection, University of Kansas, Lawrence, KS, USA (Debbie Baker and Don Huggins).

LSAM – Louisiana State Arthropod Museum, Baton Rouge, LA, USA (Victoria M. Bayless).

USNM – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Charyn Micheli).

MALUZ – La Universidad del Zulia, Maracaibo, Venezuela (Mauricio García).

MIZA – Museo del Instituto de Zoología Agrícola, Maracay, Venezuela.

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (Philip D. Perkins).

MTEC – Montana Entomology Collection, Montana State University, Bozeman, MT, USA (Michael A. Ivie).

NMHN – National Museum de Historie Naturelle, Paris, France (Antoine Mantilleri).

NMPC – National Museum, Prague, Czech Republic (Martin Fikáček)

NMW – Naturhistorisches Museum, Vienna, Austria (Manfred Jäch).

NZCS – National Zoological Collection, Suriname (Paul Ouboter).

OMNH – Oklahoma Museum of Natural History, Norman, OK, USA (Katrina Menard).

OSUC – Oklahoma State University Collection, Stillwater, OK, USA (Rick Grantham).

PQC – P. Queney Collection, Paris, France (Pierre Queney).

SEMC – Snow Entomological Collection, University of Kansas, Lawrence, KS, USA (A.E.Z. Short).

UMRM – W.R. Enns Entomology Museum, University of Missouri, Columbia, MO, USA (Robert W. Sites).

CNIN – Coleccíon Nacional de Insectos, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico (Silvia Santiago Fragoso)

WDSC – William D. Shepard Collection, California, USA (William D. Shepard).

ZMHB – Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany (Johannes Frisch).

Methods

All primary type specimens were examined, except for the types of *Lutrochus misellus*, which could not be located at NMHN, and the holotype of *Auritrochus arizonensis*, which was not loaned by the OMNH. In the latter case, paratypes from the same collecting event as the holotype and sufficient non-type material of the species was available.

Specimens were photographed using a Canon EOS 70D mounted on a Visionary Digital imaging system with individual images stacked using CombineZP image editing software (Hadley, 2010)

Specimens were relaxed in near-boiling water and male genitalia were extracted through the abdominal caudal opening. Genitalia were then cleared in KOH on a warming plate for thirty minutes, rinsed with water, and temporarily mounted in glycerin or glycerin-gelatin (Zander 1988) for observation and illustration. Genitalia were generally mounted in plain glycerin, unless

they were exceptionally curved, in which case they were mounted in the glycerin gelatin, so that the genitalia would remain in position. Illustrations were made in pen and ink using a camera lucida attached to a Olympus SZX7. For microphotographs, images were taken using a Olympus BX50 with a using an Olympus BP26 camera, and captured in Olympus Cellsens software. Images were edited in Adobe Illustrator and Adobe Photoshop. The cleared genitalia were then placed in a plastic genitalia vial below the specimen for storage.

Disarticulations for morphological study were done by relaxing the specimens in boiling water. Once softened, the hind wings were disarticulated from the body at the base using fine forceps and dry-mounted on slides using methods outlined in Kukalová-Peck and Lawrence (1993). Wing veins were homologized using terminology from Kukalová-Peck and Lawrence (1993) and Kodada and Jäch (2005).

Softened specimens were then placed in a warmed solution of KOH for 20-40 minutes to macerate the soft tissues. The specimens were then rinsed in several washes of distilled water to remove the dissolved tissues, leaving only the cleared sclerites. The sclerites were then disarticulated and arranged on a glass microscope slide in a glycerin solution.

Morphological terms used in this publication are consistent with those used in Ide *et al.* (2005). Measurements of structures are taken at the widest point using a Bioquip metric miniscale for small structures or an Illumicolor metric pocket scale for larger structures.

For scanning electron micrographs, the specimen was dehydrated in 100% ethanol and cleaned with an insect pin and fine brush. The specimen was then affixed to an SEM stub using carbon tape and coated with gold. Micrographs were taken using a Leo 1550 Scanning Electron Microscope at the Microscopy and Analytical Imaging Laboratory at the University of Kansas.

Label information is cited verbatim for type material. Line breaks are indicated by a semi-colon ";", and each individual label on the specimen is separated by quotation marks " "…" ". Additionally, primary type specimens include a label of the format "[TYPE CATEGORY] ; [Genus name, species name, author, year] ; [C.A. Maier year of designation]". Labels for holotypes are red, labels for paratypes are cyan blue, labels for lectotypes are yellow, and labels for paralectotypes are sky blue. Interpretations and corrections are indicated within brackets "[…]". Labels of holotypes, lectotypes, and taxonomically important specimens were imaged and these images are included with the figures for the species. Label information for non-type material is available in Appendix V. Data was recorded using data standards set by the author's home institution (FMNH). Label information on locality (country, primary geographic division, secondary geographic division, precise locality, latitude and longitude, elevation, body of water) and collecting event (collectors, date, habitat, event code), was recorded and associated with a unique identifier for each specimen, represented by a barcode attached to the specimen. The data in will be added to the Collections Resource for Aquatic Coleoptera online database (CReAC) at a later date.

Distribution maps were constructed using ArcGIS, and collection localities were georeferenced using a variety of sources, including gazetteers, Wikipedia, Google Earth.

Taxonomic Concepts

Species within Lutrochidae are defined by the Evolutionary Species Concept, *sensu* Wiley (1981), which states that a species is a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley & Liebermann 2011). In practice, however, it is difficult to

fully determine which species have "their own historical tendencies and evolutionary fate," based on only extant species and only museum specimens. Therefore, a combination of the Morphological Species Concept and Phylogenetic Species Concept will be used to distinguish species.

Species in the context of this study are those that are morphologically distinct, particularly those that are united by externally diagnosable characters. Molecular evidence will also guide species description, with highly supported monophyletic clades given special attention. Every attempt will be made to only describe species which are represented in collections by long series and those represented by a least 1 male, though because of the difficulty in making field collections of Lutrochidae, many "morphospecies" are represented by only singleton specimens. In cases where only a singleton is known, new species will only be described in cases where the beetle is exceptionally geographically and morphologically distinct from its congeners. This is the case with 3 species: *Lutrochus browni* **n. sp**., *L. funkae* Maier & Short 2014, and *L. gimmeli* **n. sp.**

LIST OF SPECIES

(Distributions, presented as ISO country-codes, listed in bold)

Andotrochus minutus (Maier & Short, 2013) **– BO, EC, PE, VZ**

Andotrochus cordobensis **n. sp. – AR**

Auritrochus luteus (LeConte, 1852) **– MX, US**

Auritrochus arizonicus (Brown and Murvosh, 1970) **– US**

Auritrochus brunneus **n. sp.** – **MX, GT**

Auritrochus laticeps (Casey, 1893) **– CA, US**

Auritrochus shepardi **n. sp. – MX**

Berotrochus geniculatus (Chevrolat, 1894) **– CU, HT**

Lutrochus acuminatus Grouvelle, 1889 **– VZ**

Lutrochus barrae **n. sp. – CR, PA**

Lutrochus browni **n. sp. – BR**

Lutrochus cauraensis Maier & Short, 2013 **– VZ**

Lutrochus funkae Maier & Short, 2014 **– GY**

Lutrochus germari Grouvelle, 1889 **– BR**

Lutrochus gigas Hinton, 1939a **– PE**

Lutrochus gimmeli **n. sp. – EC**

Lutrochus grenadensis Maier & Short, 2014 **– GD**

Lutrochus guarani **n. sp. – PY**

Lutrochus gustafsoni Maier & Short, 2013 **– VZ**

Lutrochus leeanneae Maier & Short, 2014 **– SR**

Lutrochus maldonadoi Maier & Short, 2013 **– VZ**

Lutrochus misellus Grouvelle, 1896 **– BR**

Lutrochus montanus Grouvelle, 1896 **– BO, EC, PE**

Lutrochus pilula Erichson, 1847 **– BR, AR**

Lutrochus tocache **n. sp. – EC, PE**

Lutrochus torrens **n. sp. – CR**

Lutrochus vestitus-group (Sharp, 1882) **– BE, CR, GT, MX, PA, VZ**

Lutrochus violaceus Maier & Short, 2013 **– VZ**

Lutrochus wao Maier & Short, 2014 **– GF, GY, VZ**

Saxitrochus meridaensis (Maier & Short, 2013) **– VZ**

RESULTS

Andotrochus Maier & Short

Type Species. *Andotrochus minutus* (Maier & Short, 2013)

Diagnosis. *Andotrochus* represents a unique body plan among Lutrochidae, with numerous characters setting it apart from the other South American lutrochids, including strongly punctate elytra (Fig. 59), pubescent mesotibiae (Fig. 72), and parameres that are not as fused as in other Lutrochid species (Fig. 73). Additionally, this genus lacks the excavations in the hypomeron and elytral epipleuron characteristic of other Lutrochidae (Fig. 58).

Description. Body length 2.4–2.6 mm; width 1.3–1.5 mm. Body ovate, dark brown to black, densely pubescent; clothed with short, fine, recumbent light golden setae and long, erect light golden setae (Fig. 56).

Head broadly rounded. Eye rounded, large, with short, golden interfacetal setae; eyes projecting slightly from outline of head (Fig. 62). Antenna short, reaching slightly past anterior border of pronotum, 11-segmented; antennomeres clothed with short golden setae (Fig. 68). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically. Apical margin of labrum straight, lacking apical setal brush. Labrum sub-rectangular, clothed with sparse, blunt setae at basal half, apical half with setae becoming sparse (Fig. 63). Mandibles large, dark brown, wedge-shaped (Fig. 64). Maxilla with 4-segmented palpus, apical palpomere

flattened and weakly triangular, truncate at apex; apical palpomere with small sensilla medially (Fig. 65). Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, two times as wide as long at base, sinuate at base, densely clothed in recumbent setae in a wavy pattern and long, erect setae (Fig. 59); lateral edges strongly convergent; pronotum with basal sublateral carinae. Lateral edge of pronotum with distinct bead, explanate apically. Posterior margin of pronotum straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, about as wide as long (Fig. 66, 60); anterior border of scutellum slightly concave. Hypomeron not excavate posteriorly (Fig. 58), lacking oblique carina. Area lateral to scutellum with distinct space between elytron and pronotum (Fig.60).

Elytron pubescent, dark brown, widest at base. Elytron slightly convex, with dense, deep, confused punctation; clothed in dense recumbent setae in a wavy pattern, and long, erect setae (Fig. 59). Elytral humerus strongly protuberant. Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 58).

Prosternum transverse, approximately as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, pointed posteriorly (Fig. 57). Metaventrite pubescent, lacking glabrous patch medially, with dispersed deep and strong punctures on disc (Fig. 67). Metaventrite with metafemoral lines broadly separated from the katepisternal suture, lacking distinct mesotarsal rests. Mesepisternum and mesepimeron continuous, not excavate to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae. Wing venation reduced. (Fig. 61).

Legs long and slender. Profemur densely pubescent. Protibia entirely pubescent. Protarsus with all tarsomeres pubescent, clothed with dense, golden setae; apical tarsomere as

long as preceding four tarsomeres combined. Mesocoxa lacking tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia predominantly pubescent, lacking excavation for mesotarsi. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere almost as long as preceding four tarsomeres combined. Plate of metacoxa strongly excavate medially (Fig. 57). Metatrochanter globose, without posterior extensions (Fig. 70). Metafemur densely pubescent.

Abdomen densely pubescent, with five ventrites. First ventrite shallowly excavated for reception of folded hind legs (Fig. 71); metacoxal rests on first ventrite each with two deep, wax-filled pits (Fig. 71). Apical ventrite broadly rounded.

Aedeagus slender and curved, becoming more curved at tapered tip. Parameres only slightly fused, pointed, with distinct lobes interiorly subapically (Fig. 73).

Etymology. The generic name *Andotrochus* is derived from the Andes mountains, in reference to the mountainous habitats of this genus, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. These two species are removed from *Lutrochus* and placed into a separate genus based on its distinctive morphology and putative ecological differences. Given their distinctive habitus, which bears striking superficial resemblance to the Limnichidae, *Andotrochus* has historically been misidentified. In fact, three water beetle specialists (CAM, Harley P. Brown, and Paul J. Spangler), on separate occasions, identified specimens of *A. minutus* as "Limnichidae new genus." It was not until the specimens were examined more closely, that the characters placing them in Lutrochidae were recognized.

It is known from throughout the area surrounding the Andean belt, though not necessarily at high elevations, from western Venezuela south to Bolivia and Argentina. These are often

found at UV lights, though their habitat appears to be in waterlogged debris is streams, as there is a series of specimens collected from "trash" in the Rio Surutu, Bolivia (H. P. Brown, in. litt.).

Comparative Notes. Despite its deceptive superficial similarity to Limnichidae, the genus possesses the necessary synapomorphies which place it in Lutrochidae – expanded apical maxillary palpomeres (Fig. 65), short, clavate antennae (Fig. 68), and interfacetal setae (Fig. 62) all point clearly to its place in Lutrochidae.

***Andotrochus cordobensis* Maier & Short n. sp.**

(Figs. 48–55)

Type Material. Holotype female: "ARGENTINA NC; N of Cordoba; W of Ascochinga; Sierra de Cordoba; 7.I.2010 Snižek". Holotype deposited in EMEC (Figs. 53 & 54). **Paratype female (1): ARGENTINA: Cordoba Prov:** Same locality data as holotype. Paratype will be deposited in: 1 in EMEC.

Diagnosis. This species most closely resembles its only congener, *Andotrochus minutus*. *Andotrochus cordobensis* can be distinguished the previous species by its possession of the following combination of characters: body pilosity short, punctuation of the elytra fine, without distinct puncture rows, hind tarsi completely glabrous, and the mesotibia with a narrow longitudinal glabrous band dorsally.

Description. HOLOTYPE FEMALE. – Length 3.2 mm Width 1.7 mm; clothed with short, fine, recumbent light golden setae, dorsal setae with distinct wavy pattern (Fig. 48).

Head broadly rounded. Eye rounded, medium, with short, golden interfacetal setae; eyes projecting slightly from outline of head. Antenna very short, barely reaching posterior border of eye, reddish-brown and clavate; apical nine antennomeres short, clothed with short golden setae

(Fig. 52). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of short setae apically. Apical margin of labrum gently curved, and glabrous, lacking apical setal brush. Labrum clothed with sparse, blunt setae at basal half, apical half glabrous. Mandibles large, dark brown, falciform; apex of mandible with two teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and weakly triangular, truncate at apex. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, two times as wide as long at base, weakly sinuate at base, densely clothed in recumbent setae in a wavy pattern and short, erect setae (Fig. 48); lateral edges strongly convergent. Lateral edge of pronotum with distinct bead, explanate apically. Posterior margin of pronotum straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, slightly wider than long (Fig. 48). Hypomeron excavate posteriorly, excavate only in posterior quarter (Fig. 49). Area lateral to scutellum with distinct space between elytron and pronotum.

Elytron pubescent, dark brown, widest in anterior third. Elytron convex, with dense, shallow, confused punctation; clothed in dense recumbent setae in a wavy pattern, and short, erect setae (Fig. 48). Elytral humerus not protuberant. Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 50). Elytral apex strongly acuminate (Fig. 50).

Prosternum transverse, slightly wider than long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process slightly longer than wide, with bead laterally, rounded posteriorly (Fig. 50). Mesoventrite pubescent. Mesepisternum and mesepimeron continuous, not excavate to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender. Profemur densely pubescent, reddish-brown, becoming dark brown distally. Protibia entirely pubescent, entirely dark brown. Protarsus reddish brown, proximal four tarsomeres pubescent; apical tarsomere with sparse setae proximally; apical tarsomere as long as preceding four tarsomeres combined (Figs. 52 & 55). Mesocoxa lacking tuft of long golden setae basally. Mesofemur reddish brown, becoming dark brown distally, densely pubescent posteriorly, becoming less so anteriorly (Fig 50). Mesotibia dark brown, entirely pubescent, with narrow longitudinal glabrous band, which widens to encircle entire tibia at distal end (Fig. 55). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere almost as long as preceding four tarsomeres combined (Fig. 50). Metatrochanter globose, with slight posterior projection. Metafemur densely pubescent. Metatibia almost entirely pubescent, with narrow longitudinal glabrous band dorsally (Fig. 55). Metatarsus glabrous. Apical metatarsomere longer than previous four combined.

Abdomen densely pubescent, with five ventrites. First ventrite shallowly excavated for reception of folded hind legs (Fig. 50), with four very shallow pits just posterior to the metacoxae (Fig 49). Apical ventrite broadly rounded.

Ovipositor as illustrated (Fig. 73).

Male. The male of this species is unknown.

Intraspecific Variation. This species is known from only two specimens, so an adequate survey of variation in this species could not be conducted. Based on observations of other species, specimens may vary slightly in color, from dark brown to medium brown, as well as size (the paratype is 3.1 mm long by 1.6 mm wide). Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named "cordobensis" in reference to its type locality in the Sierra de Córdoba, Argentina.

Habitat and Distribution. This species is known from only a single locality, collected by Miroslav Snížek in the Sierras Chicas in Argentina (Fig. 19).

Remarks. This species, and others like it, may be more common in Argentina. Coleopterist Juan Enrique Barriga-Tuñon has recorded three morphospecies of Lutrochidae from Argentina, two of which closely resemble *A. cordobensis* (Barriga-Tuñon, 2015).

While it differs significantly from its congener, *A. minutus*, *A. cordobensis* still possesses a suite of characters which place it in *Andotrochus*, including the four pits on the first abdominal ventrite (though they are shallower in *A. cordobensis*), recumbent wavy setae, pubescent mesotibiae, and mesotibiae lacking excavation at apex.

***Andotrochus minutus* (Maier & Short, 2013)**

Lutrochus minutus Maier & Short, 2013

(Figs. 56–75)

Type Material. Holotype male: "VENEZUELA: Tachira State;7° 35.038′ N, 72° 10.340′ W, 472 m; El Tama National Park; 16.vii.2009; leg. Short, Sites, Garcia, Inciarte; Gustafson & Camacho;HG-vapor light VZ09-0716-07A" "SEMC0876083;KUNHM-ENT". Holotype deposited in MIZA. **Paratypes (9): VENEZUELA: Tachira State:** Same locality data as holotype. Paratypes will be deposited in: 1 in MIZA, 1 in MALUZ, 1 in NMW, 5 in SEMC, and 1 in USNM.

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species is smaller than any other described Lutrochidae in South America, but most closely resembles *Saxitrochus meridaensis*, but can be distinguished from that species by the following combination of characters: metaventrite without medial circular glabrous patch (Fig. 57); scutellum triangular (Fig. 60); elytral punctation dense, confused (Fig. 59); and apical maxillary palpomere wide (Fig. 65).

Description. MALE. – Length 2.4 mm; width 1.3 mm. Body ovate, dark brown to black, densely pubescent; clothed with short, fine, recumbent light golden setae and long, erect light golden setae (Fig. 62).

Head broad, broadly rounded. Eye rounded, large, with very long, golden interfacetal setae; eyes projecting slightly from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 segments short, reddish-brown and clavate, clothed with short golden setae (Fig. 62). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically. Apical margin of labrum straight, lacking apical setal brush. Labrum clothed with sparse, blunt setae at basal half, apical half glabrous. Mandibles large, dark brown, falciform; apex of mandible with two teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and weakly triangular, truncate at apex. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, two times as wide as long at base, sinuate at base, densely clothed in recumbent setae in a wavy pattern and long, erect setae (Fig. 56); lateral edges strongly convergent. Lateral edge of pronotum with distinct bead, explanate apically. Posterior margin of pronotum straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, about as wide as long (Fig. 60). Hypomeron not excavate posteriorly (Fig. 58). Area lateral to scutellum with distinct space between elytron and pronotum (Fig. 60).

Elytron pubescent, dark brown, widest at base. Elytron slightly convex, with dense, deep, confused punctation; clothed in dense recumbent setae in a wavy pattern, and long, erect setae (Fig. 59). Elytral humerus strongly protuberant. Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 57). Elytral apex strongly acuminate (Fig. 58).

Prosternum transverse, approximately as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, pointed posteriorly(Fig. 57). Mesoventrite pubescent. Mesepisternum and mesepimeron continuous, not excavate to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender. Profemur densely pubescent, reddish-brown, becoming dark brown distally. Protibia entirely pubescent, entirely dark brown. Protarsus reddish brown, with all tarsomeres pubescent, clothed with dense, golden setae; apical tarsomere as long as preceding four tarsomeres combined. Mesocoxa lacking tuft of long golden setae basally. Mesofemur reddish brown, becoming dark brown distally, densely pubescent posteriorly, becoming less so anteriorly (Fig 72). Mesotibia dark brown, entirely pubescent, with narrow glabrous band posteriorly (Fig. 72). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere almost as long as preceding four tarsomeres combined (Fig 72). Metatrochanter globose, without posterior extensions. Metafemur densely pubescent. Metatibia entirely pubescent. Metatarsus pubescent, with pubescence becoming more sparse near apex. Apical metatarsomere nearly as long as previous four combined.

Abdomen densely pubescent, with five ventrites. First ventrite shallowly excavated for reception of folded hind legs (Fig. 71), with four distinct, wax-filled, deep pits just posterior to metacoxae (Fig. 58). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.1 mm long, strongly curved. Aedeagus slender and curved, becoming more curved at tapered tip. Parameres slightly fused, pointed, with distinct lobes interiorly subapically (Fig. 73).

Female. Length 2.4 mm; width 1.4 mm. Externally similar to male, females generally larger than males. Elytral apices more rounded (Fig. 56).

Intraspecific Variation. This species varies only slightly in size, ranging from 2.4–2.6 mm long and 1.3–1.5 mm wide. Additionally, specimens vary slightly in color, from dark brown to medium brown. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named "minutus" referring to its status as the smallest known lutrochid described from South America.

Habitat and Distribution. This species is known from throughout Andean South America, and the type locality is Tachira State, Venezuela (Fig. 20). Little is known of the biology or habits of species in this genus, as all individuals were collected either at mercury vapor or UV lamps. Field notes from Harley P. Brown (deceased, OMNH) indicate that adults of the closely related species, *A. minutus*, in Bolivia may live in water-splashed detritus, much like laraine Elmidae in the genus *Phanocerus* (Brown, *in litt.*).

Auritrochus Maier & Short

Type Species

Auritrochus luteus (LeConte, 1852)

Diagnosis. This genus is distinct, but most closely resembles *Berotrochus* in vestiture of legs, and possesses the following suite of characters which separate it from all other genera: body form strongly wedge-shaped, with a distinctive golden sheen (Figs. 76 & 121); antennae short, reaching no further than half-way down pronotum (Figs. 100 & 122); head lacking two rugose patches at occiput; mandibles large and sickle-shaped; mesotibiae lacking excavation for reception of mesotarsi (Fig. 132); mesotibia completely glabrous (Figs. 125 & 123); parameres of male genitalia broadly joined to tegmen; tegmen elongate and strongly curved (Fig. 102). Specimens of *Auritrochus* are also significantly smaller than members of *Lutrochus* and *Berotrochus*, ranging in size from 3.0 mm to 4.9 mm in length.

Description. Body length 3.0–4.9 mm and body width 1.3–2.6 mm. Body strongly wedge-shaped, golden metallic to light brown in color, densely pubescent; completely clothed with setae (Fig. 99).

Head broadly rounded, deflexed ventrally, grooved beneath eye for reception of antenna. Eye rounded, with short golden interfacetal setae; eyes strongly projecting to smooth within outline of head. Antenna short, barely reaching anterior border of pronotum (Figs. 100 & 122), clothed with short, golden setae. Mouth strongly hypognathus. Frontoclypeal suture indistinct. Clypeal margin strongly curved, clothed with setae (Fig. 100). Labrum evenly clothed with recumbent setae, lacking transverse row of long setae at midline (Fig. 114). Mandible large, narrow, dark brown, sickle-shaped, often with only one broad, distinct tooth apically (Fig. 110). Maxilla with 4-segmented palpus, apical palpomere flattened and sub-cylindrical, greatly expanded at apex (Figs. 113). Labial palpus 3-segmented; apical palpomere sub-cylindrical, with field of sensillae at apex (Fig. 112).

Pronotum pubescent, weakly bisinuate at base (Fig. 99); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, not explanate to slightly explanate laterally at base (Fig. 101). Posterior margin straight or only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum convex (Fig. 101). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur (Fig. 101).

Elytron pubescent, brown to brownish-black, with distinct golden sheen, widest at base of elytron. Elytron strongly convex, strongly wedge-shaped, broadly rounded; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent or erect setae; humerus strongly protuberant (Fig. 99). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 100). Elytral apex rounded to acuminate.

Prosternum transverse, approximately twice as wide as long, deflexed or not deflexed to accommodate head; prosternal process acute or rounded posteriorly. Metaventrite entirely pubescent; metafemoral lines nearly confluent with katepisternal suture, with distinct mesotarsal rests (Fig. 108). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 101).

Legs long and slender. Profemur densely pubescent, protibia entirely pubescent (Fig. 107). Protarsus with at least first four tarsomeres tomentose, particularly ventrally; apical tarsomere with varying degrees of setation. Mesofemur densely pubescent. Mesotibia entirely glabrous, mesotibia smooth, not expanded, with apex smooth, lacking excavation for reception of mesotarsus (Fig. 116). Mesotarsus glabrous (Fig. 107). Metatrochanter excavate for reception of metatibia, with weak or no posterior projection (Fig. 100). Metafemur densely pubescent. Metatibia entirely tomentose, except for small bare patch at apex. Metatarsus with first four

tarsomeres entirely tomentose; apical metatarsomere with varying degrees of setation (Figs. 107 & 82).

Abdomen entirely pubescent, with five ventrites, ventrites constricted medially (Fig. 77). Metacoxal rests on first ventrite extending half to two thirds of the way to second ventrite. First ventrite excavated for reception of hind legs. Apical ventrite of male rounded to very shallowly notched (Fig. 77).

Male genitalia as illustrated, tegemen elongate, narrow, and strongly curved parameres pointed and broadly joined to basal piece (Fig. 102). Aedeagus strongly curved. Parameres nearly completely fused.

Comparative Notes. Morphologically, *Auritrochus* bears many similarities with *Andotrochus,* including its small size and metallic sheen. Interestingly, the ovipositors in both *Auritrochus* and *Andotrochus* are similar, with a blunt apex instead of a strongly sickle shaped apex, as in *Lutrochus*. The elongate and pointed apex in *Lutrochus* may be the result of an adaptation to ovipositing in waterlogged wood and need to be able to insert the eggs into the crevices in wood. Both *Auritrochus* and *Andotrochus* lack the apical excavation of the mesotibia.

Ecologically, *Auritrochus* and *Berotrochus* occupy similar niches in their ranges, with both genera preferring high-calcium travertine streams – *Auritrochus* in North and Central America, and *Berotrochus* in the Greater Antilles.

Biology and Distribution. The five species of *Auritrochus* are found throughout the northern part of the Western Hemisphere, from southern Canada to Belize – (with a dubious singleton from Costa Rica in OMNH collection).

Auritrochus can be found in fast flowing rivers and streams in areas of high calcium (limestone & karst topography). Within these habitats, the adult beetles live on watersplashed

rocks, detritus, and mosses, and they are almost never completely submerged. This genus can be locally abundant, with hundreds of adult beetles aggregating as the water's edge in spring and summer. They are not well represented in collections, though, as this habitat is only rarely tapped for aquatic insect collections. More biological information can be found in the individual species accounts.

***Auritrochus arizonicus* (Brown & Murvosh, 1970)**

(Figs. 76–91)

Lutrochus arizonicus Brown & Murvosh, 1970

Type Material. Holotype: Same data as paratypes, deposited at OMNH. [The holotype was not examined in this study]. **Paratypes** (3): "Sedona, Arizona; 69-6-12 C. Murvosh [white label, handwritten]" "Lutrochus; arizonicus; det. HPB; Paratype [white label, handwritten]" "Catalog No. OMNH-100852" (Figs. AURARI7, 91). Deposited in OMNH.

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Auritrochus arizonicus* is externally distinct from other species of *Auritrochus*, with the prosternum not deflexed to accommodate head; mesotibia with short tomentose patch at base; large size (3.0–4.3mm); and distinctive male genitalia (Fig. 79). It is also the only species of *Auritrochus* that occurs in far southwestern United States (Central Arizona).

Redescription. PARATYPE MALE. – Length 3.0 mm; width 1.7 mm. Body wedge-shaped and strongly convex, brown to black with a golden to greenish sheen, densely pubescent; clothed short, recumbent, golden setae (Figs. 76, 77 & 78).

Head broad, frons flattened, weakly grooved beneath eye for reception of antenna (Fig. 78). Eye rounded, large, with short, golden interfacetal setae; eyes strongly projecting from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown and testaceous at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin strongly curved, with brush of long setae apically, setae not reaching apex of labrum. Apical margin of labrum sinuate, with apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with dense, short, golden setae. Mandibles large, dark brown, sickle-shaped; apex of manidible with one broad, flattened tooth (Fig. 85). Maxilla with 4-segmented palpus, apical palpomere sub-cylindrical, but expanded at apex, almost 1.25 times as wide as long, rounded at apex (Fig. 89). Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, more than two times as wide as long at base, weakly bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 78). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum extremely convex (Fig. 76). Scutellum triangular, a little wider than long. Hypomeron excavate posteriorly to accommodate femur.

Elytron pubescent, dark brown with metallic green sheen, widest near base. Elytron broadly convex, with dense, small punctures, lacking puncture striae; humerus strongly protuberant (Fig. 76). Lateral edge with distinct bead (Fig. 78), epipleuron not expanded, not appearing broad in ventral aspect (Fig. 77). Elytral apex slightly acuminate (Fig. 76).

Prosternum transverse, approximately twice as wide as long; strongly deflexed to accommodate withdrawn head, with strong transverse fold anteriorly; anterior edge with strong bead (Fig. 77). Prosternal process about 1.5 times as wide as long, lacking bead laterally, acute

posteriorly (Fig. 77), lateral edges weakly divergent. Mesoventrite pubescent, lacking glabrous patch (Fig. 77). Metaventrite with metafemoral lines convergent with katepisternal suture, lacking distinct mesotarsal rests (Fig. 83). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly entire length of metacoxae.

Legs long. Profemur densely pubescent. Protibia pubescent, except for small bare patch apically. Protarsus with basal four tarsomeres tomentose, especially pubescent ventrally; apical tarsomere as long as preceding four tarsomeres combined, setose basally, glabrous apically (Fig. 82). Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, with few scattered setae, with small patch of golden setae at apex, setose patch extending one eighth the length of tibia; apex lacking excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with distinct rounded projection posteriorly. Metatrochanter globose, with single short hook-like posterior extension proximally (Fig. 80). Metafemur densely pubescent. Metatibia pubescent for entire length (Fig. 82). Metatarsus almost entirely glabrous, except pubescent in small triangular patch at base (Fig. 82).

Abdomen densely pubescent, with five ventrites; ventrites constricted medially. First ventrite very shallowly excavated for reception of folded hind legs (Fig. 77). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 1.9mm long (Fig. 79). Aedeagus slender and curved evenly to apex, abruptly narrowing near apex. Parameres fused, pointed, with minimally extended apex in lateral aspect.

Female. Length 4.0 mm; width 2.0 mm. Externally similar to male, females generally larger than males; abdominal ventrites of female not constricted medially; apical abdominal ventrite pointed (Fig. 80).

Intraspecific Variation. This species varies considerably in size, ranging from 3.0–4.3 mm long and 1.7–2.3 mm wide. Additionally, specimens vary slightly in color – from light metallic gold to dark black-brown; specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease. Specimens also vary a surprising amount in body shape, with some specimens having a stronger wedge shape than others, and pronotal lateral borders with varying degrees of convergence.

Habitat and Distribution. Brown (1987) notes that the adults of this species are riparian, and are rapid fliers further details on the biology of the species are described in the aforementioned publication.

This species ranges throughout karstic areas of North-Central Arizona (Fig. 21).

Remarks. *Auritrochus arizonicus* represents a disjunct species of Lutrochidae, as it is the only species of Lutrochidae that occurs in Central Arizona. Its nearest relative, *Auritrochus luteus*, range stops in the Southern High Plains of Southeastern New Mexico. While this gap may be explained by lack of sampling, a quick examination of a map of karst regions of the US reveals that the land area between the two species' ranges is not karstic, and the habitat is likely unsuitable for *Auritrochus* spp.

***Auritrochus brunneus* Maier & Short n. sp.**

(Figs. 92–98)

Type Material. Holotype, male: "MEXICO: Veracruz; Los Tuxtlas area, Rio; Palma above La Palma; 13 May 1981, Blk. Lite; Paul J. Spangler [PJS-MX-810507-3]" Holotype deposited in USNM (Figs. 97 & 98). **Paratypes** (53): Same locality data as holotype (22 specimens). "MEXICO: Veracruz; Los Tuxtlas area, Rio; Palma above La Palma; 7 May1981, PJSpangler; & Silvia Santiago" (22 specimens). "MEXICO: Veracruz; Los Tuxtlas area, Rio; Palma above La Palma; 7-14 May 1981; C.M. & O.S. Flint, Jr." (2 specimens). "MEXICO: Veracruz; Los Tuxtlas area, Rio; Palma above La Palma; 15 May 1981; P.J. Spangler." (7 specimens). Deposited in USNM, 2 specimens in CNIN.

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Auritrochus brunneus* has the smallest average size of all *Auritrochus* (body length 3.5–2.4 mm long, it is also the most consistently dark brown *Auritrochus* species (Fig. 92–94). However, *A. brunneus* can also be distinguished by its distinctive genitalia, and unique setation pattern of the apical metatarsomere (nearly completely glabrous). It is also one of the species of *Auritrochus* with the southernmost distribution, occuring throughout southern Mexico.

Description. HOLOTYPE MALE. – Length 2.7 mm; width 1.4 mm. Body weakly wedge-shaped and strongly convex, brown to black with a only a slight bronze sheen, densely pubescent; clothed short, recumbent, brown setae (Figs. 92–94).

Head broad, frons sinuate, weakly grooved beneath eye for reception of antenna. Eye rounded, large, with short, brown interfacetal setae; eyes only slightly projecting from outline of

head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin strongly curved, with brush of long setae apically, setae not reaching apex of labrum. Apical margin of labrum sinuate, with apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with dense, short, brown setae. Mandibles large, dark brown, sickle-shaped; apex of manidible with one broad, flattened. Maxilla with 4-segmented palpus, apical palpomere sub-cylindrical, but expanded at apex, almost as wide as long, rounded at apex. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, nearly two times as wide as long at base, weakly bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 94). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum weakly convex (Fig. 92). Scutellum triangular, a distinctly wider than long. Hypomeron not excavate posteriorly to accommodate femur (Fig. 94).

Elytron pubescent, dark brown with slight bronze sheen, widest near base. Elytron broadly convex, with dense, small punctures, lacking puncture striae; humerus only weakly protuberant (Fig. 92). Lateral edge with distinct bead (Fig. 94), epipleuron not expanded, not appearing broad in ventral aspect (Fig. 93). Elytral apex slightly acuminate (Fig. 92).

Prosternum transverse, approximately 1.5 times as wide as long; strongly deflexed to accommodate withdrawn head, with strong transverse fold anteriorly; anterior edge with strong bead (Fig. 93). Prosternal process about 1.5 times as wide as long, with distinct bead laterally; process acute posteriorly (Fig. 93), lateral edges weakly divergent. Mesoventrite pubescent, lacking glabrous patch (Fig. 93). Metaventrite with metafemoral lines convergent with katepisternal suture, lacking with distinct mesotarsal rests (Fig. 93). Mesepisternum and

mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly entire length of metacoxae.

Legs long. Profemur densely pubescent. Protibia pubescent, except for small bare patch apically. Protarsus with basal four tarsomeres tomentose, especially pubescent ventrally; apical tarsomere shorter than preceding four tarsomeres combined, setose basally, glabrous apically. Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, with few scattered setae, with small patch of brown setae at apex, setose patch extending one sixteenth length of tibia; apex lacking excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with distinct rounded projection posteriorly. Metatrochanter globose, with single short hook-like posterior extension proximally (Fig. 93). Metafemur densely pubescent. Metatibia pubescent for entire length (Fig. 93). Metatarsus almost entirely glabrous, except pubescent in small triangular patch at base.

Abdomen densely pubescent, with five ventrites; ventrites constricted medially. First ventrite very shallowly excavated for reception of folded hind legs (Fig. 93). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 0.6mm long (Fig. 96). Parameres less fused than in other species of *Auritrochus*, showing small gap between basal piece and paramere (Fig. 96). Aedeagus slender and curved evenly to apex. Parameres fused, pointed, with extended, rounded apex in lateral aspect.

Female. Length 3.5 mm; width 1.9 mm. Externally similar to male, females generally larger than males; abdominal ventrites of female not constricted medially; apical abdominal ventrite pointed.

Intraspecific Variation. This species varies considerably in size, ranging from 2.4–3.5 mm long and 1.3–2.4 mm wide. Additionally, specimens vary slightly in color – from light reddish-brown to dark reddish-brown, specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease. Specimens vary little body shape, with nearly all specimens being broadly rounded, and pronotal lateral borders with varying degrees of convergence.

Etymology. This species is named "*brunneus*" in reference to its brownish color.

Habitat and Distribution. The type series was collected in a sunny stream running through an area with reddish volcanic soil. Interestingly, no mention is made in the original field notes of this locality having karstic geology. Adults were observed aggregating on water-splashed rocks emerging from the river (CReAC, 2015)

The largest series (and the type series) was collected at Rio La Palma, in Veracruz State, Mexico. Single specimens have been collected throughout southern Mexico and Guatemala, however (Fig. 22).

***Auritrochus laticeps* (Casey, 1893)**

(Figs. 99–120)

Lutrochus laticeps Casey, 1893

Type Material. *Lutrochus laticeps:* Type series deposited in USNM, Casey Collection. **Holotype:** [Point mounted.] “Mich.” “CASEY; bequest; 1925” “TYPE USNM; 49216[red label]” “Lut; laticeps [handwritten].” “USNM ENT; 00776574” “LECTOTYPE; *Lutrochus laticeps*; Casey 1893; des. Maier & Short 2015”. (Figs. 103-106) **Paratypes (13):** Same data as holotype (1 specimen, USNM, Casey Collection). “L.” (12 specimens, USNM, Casey Collection).

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Auritrochus laticeps* is externally distinct from other species of *Auritrochus*, with the prosternum not deflexed to accommodate head; mesotibia with only very short tomentose patch at base; metaventrite with metafemoral lines nearly convergent with katepisternal suture, with distinct mesotarsal rests (108); smaller size (3.7–2.3 mm); and distinctive male genitalia (Fig. 102). It is also the only species of *Auritrochus* that occurs in the Eastern United States.

Redescription. HOLOTYPE MALE. – Length 3.2 mm; width 1.7 mm. Body wedge-shaped and strongly convex, black with a golden to greenish sheen, densely pubescent; clothed short, recumbent, golden setae (Figs. 99, 100 & 101).

Head broad, frons weakly concave, head weakly grooved beneath eye for reception of antenna (Fig. 101). Eye rounded, large, with short, golden interfacetal setae; eyes strongly projecting from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown and testaceous at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin curved, with brush of long setae apically, setae not reaching apex of labrum. Apical margin of labrum broadly rounded, with short apical setae, lateral setae as long as medial setae. Labrum clothed with

dense, short, golden setae. Mandibles large, dark brown, sickle-shaped; apex of manidible with one broad, flattened tooth (Fig. 110). Maxilla with 4-segmented palpus, apical palpomere sub-cylindrical, but expanded at apex, almost 1.5 times as wide as long, rounded at apex (Fig. 113). Labial palpus 3-segmented; apical palpomere cylindrical, slightly widened apically (Fig. 112).

Pronotum pubescent, more than two times as wide as long at base, weakly bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 101). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum extremely convex (Fig. 99). Scutellum triangular, as wide as long. Hypomeron excavate posteriorly to accommodate femur.

Elytron pubescent, dark brown with metallic green sheen, widest near base. Elytron broadly convex, with dense, small punctures, lacking puncture striae; humerus strongly protuberant (Fig. 99). Lateral edge with distinct bead (Fig. 101), epipleuron not expanded, not appearing broad in ventral aspect (Fig. 100). Elytral apex slightly acuminate (Fig. 99).

Prosternum transverse, approximately twice as wide as long; not deflexed to accommodate withdrawn head, lacking strong transverse fold anteriorly; anterior edge with strong bead (Fig. 100). Prosternal process about 1.5 times as wide as long, lacking bead laterally, acute posteriorly (Fig. 100), lateral edges parallel. Mesoventrite pubescent, lacking glabrous patch (Fig. 100). Metaventrite with metafemoral lines nearly convergent with katepisternal suture, with distinct mesotarsal rests (Fig. 108). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly entire length of metacoxae.

Legs long. Profemur densely pubescent. Protibia pubescent. Protarsus with basal four tarsomeres tomentose, especially pubescent ventrally; apical tarsomere as long as preceding four

tarsomeres combined, setose basally, for more than ½ length, glabrous apically (Fig. 107). Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, with few scattered setae, with small patch of golden setae at apex, setose patch only at very base of tibia; apex lacking excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta arising from fourth tarsomere; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa with distinct rounded projection posteriorly. Metatrochanter globose, with distinct posterior face (Fig. 115). Metafemur densely pubescent. Metatibia pubescent for entire length (Fig. 107). Apical metatarsomere glabrous on apical half (Fig. 107).

Abdomen densely pubescent, with five ventrites; ventrites constricted medially. First ventrite not excavated for reception of folded hind legs (Fig. 111). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 1.9mm long (Fig. 102). Aedeagus slender and strongly curved to apex. Parameres fused, pointed, with extended apex in lateral aspect.

Female. Length 3.7 mm; width 2.3 mm. Externally similar to male, females generally larger than males; abdominal ventrites of female not constricted medially; apical abdominal ventrite pointed (Fig. 80).

Intraspecific Variation. This species varies considerably in size, ranging from 2.3–3.7 mm long and 1.4–2.3 mm wide. Additionally, specimens vary slightly in color – from light metallic bronze to dark metallic bronze, specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down

with grease. Specimens also vary a surprising amount in body shape, with some specimens having a stronger wedge shape than others, and pronotal lateral borders with varying degrees of convergence.

Habitat and Distribution. *Auritrochus laticeps,* is known from throughout the eastern US and Canada (Fig. 23) and has far more varied habitat preferences than other species of *Lutrochus*, occurring in fast-flowing streams, even those that lack the specific karst topography preferred by other species, and on water-splashed rocks at the edge of lakes. They do appear to be restricted in range to only landscapes which predominantly have carbonitic limestones, though.

One of the most prolific localities in the Northeastern United States is actually an island on Lake Erie, at Put-In-Bay, Ohio. On this island, adult beetles can be found on warm summer days climbing on beach wrack and on water-splashed rocks at the margin of Lake Erie (M.A. Ivie pers. comm.)

In contrast to the other species of Lutrochidae in the Neotropics, which are active year-round, adults of the three North American species are highly periodical, as they are only active from late May to early September. *Auritrochus laticeps* is widespread in Eastern North America, from southern Canada, to Missouri and northeastern Oklahoma, and probably has the widest geographic range of any species of *Auritrochus* (Roughley and Larson 1991, Brown 1976). Throughout their range, *A. laticeps* has varied habitat preferences, with one thing in common – they prefer to be in the boundary area where fast-flowing water splashes on debris, moss, or rocks. Adult beetles may be found flying around and resting on moist leaf packs and debris dams in rivers and streams (Spavinaw Creek, OK, pers. obs. & museum specimens) (Fig. 120) and on

wave-splashed rocks on the Great Lakes (Put-in-Bay, OH, museum specimens). These habits are similar to those of *Psephenus herricki* (DeKay, 1844) and the two are often collected together.

At the borders of their range, *Auritrochus laticeps* can be quite difficult to find. In Kansas, despite extensive sampling of Kansas rivers and streams by entomologists at the University of Kansas (KU) and the Kansas Biological Survey [KBS] (2,058 collecting events for Aquatic Coleoptera in Kansas as of 2 June 2014), *Auritrochus laticeps* has not been collected in the state since 1920 (CReAC 2014). A single specimen was collected by Dr. William E. Hoffman, former Assistant Curator of Entomology at KU, from Neosho County, with no further locality or habitat information. This is typical, however, as the unique habitat preferences of *Auritrochus laticeps* prevents them from being collected in both general benthic samples and with terrestrial collecting methods. Indeed, this observation was confirmed when intense benthic sampling by four collectors in typical riffle and run habitat below Elk Falls (Elk Co., Kansas) yielded a variety of aquatic beetles, including several species of *Stenelmis* (Elmidae) and *Gyretes* (Gyrinidae), but no *A. laticeps*. Once the appropriate habitat was found at Elk Falls, travertine beetles were present in great abundance.

The Elk River at Elk Falls is located in a riparian woodland in corn/wheat/soybean farmland at the edge of the Flint Hills, in Elk County, Kansas (Figs. 117–119). The waterfall (37.374416, -96.184123) is formed at the edge of a Shawnee Group limestone formation, where it erodes away the neighboring shale. The rock at the falls is covered in dense green algae and ample log jams from woody debris and rubble are present (Figs. 118). *Auritrochus* adults were found taking shelter and grazing on algae and moss on the water-splashed vertical rock faces of the falls, nestled in crevices in algae-covered logs, and in wet (but not submerged) leaf-packs (Fig. 118) slower moving riffles and runs did not produce any specimens.

Remarks. *Auritrochus laticeps* was described by Casey in 1893, from a series of specimens that includes individuals (deposited in the USNM) from throughout the Eastern US. A holotype specimen was not designated in the publication, however Casey stated that the type is from "Michigan" and a single specimen, USNM 49216 has a label that indicates "Type" (Figs. 103 & 104) This specimen, presumably labeled by Casey himself, is the holotype specimen.

***Auritrochus luteus* (LeConte, 1853)**

(Figs. 121–140)

Lutrochus luteus LeConte, 1853

Type Material. Holotype, male. [Point mounted.] "Fort Gates; Tex. [handwritten]" "J. L. Leconte; Coll." "Type 2264; [Red paper]" "Lutrochus; luteus; Lec.; Holo" [red dot label]. (Fig. 124) **Paratype (1):** Same data as holotype. Deposited in MCZ, type photos can be found in the MCZ online type database.

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Auritrochus luteus* is externally distinct from other species of *Auritrochus*, with the prosternum strongly deflexed to accommodate head; mesotibia with lacking tomentose patch at base; metaventrite with metafemoral lines nearly convergent with katepisternal suture, with distinct mesotarsal rests (Fig. 126); larger size (3.9–2.2 mm) in length; and distinctive male genitalia (Fig. 124).

Redescription. HOLOTYPE MALE. – Length 3.6 mm; width 2.1 mm. Body wedge-shaped and strongly convex, golden in color with a golden to greenish metallic sheen, densely pubescent; clothed short, recumbent, golden setae (Figs. 121, 122 & 123).

Head broad, frons flat concave, head weakly grooved beneath eye for reception of antenna (Fig. 123). Eye rounded, large, with short, golden interfacetal setae; eyes strongly projecting from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown and testaceous at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin curved, with brush of long setae apically, setae not reaching base of labrum. Apical margin of labrum broadly rounded, with short apical setae, lateral setae as long as medial setae. Labrum clothed with dense, short, golden setae. Mandibles large, dark brown, sickle-shaped; apex of manidible with one broad, flattened tooth (Fig. 131). Maxilla with 4-segmented palpus, apical palpomere sub-cylindrical, but expanded at apex, nearly 2 times as long as wide, rounded at apex (Fig. 130). Labial palpus 3-segmented; apical palpomere cylindrical, slightly widened apically.

Pronotum pubescent, more than two times as wide as long at base, weakly bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 123). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum extremely convex (Fig. 121). Scutellum triangular, slightly wider than long. Hypomeron excavate posteriorly to accommodate femur.

Elytron pubescent, golden in color with metallic green sheen, widest near base. Elytron broadly convex, with dense, small punctures, lacking puncture striae; humerus strongly protuberant (Fig. 121). Lateral edge with distinct bead (Fig. 123), epipleuron not expanded, not appearing broad in ventral aspect (Fig. 122). Elytral apex slightly acuminate (Fig. 121).

Prosternum transverse, approximately twice as wide as long; strongly deflexed to accommodate withdrawn head, with strong transverse fold anteriorly; anterior edge with strong bead (Fig. 122). Prosternal process about as wide as long, lacking bead laterally, acute

posteriorly (Fig. 122), lateral edges strongly divergent. Mesoventrite pubescent, lacking glabrous patch (Fig. 122). Metaventrite with metafemoral lines nearly convergent with katepisternal suture, with distinct mesotarsal rests (Fig. 126). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly entire length of metacoxae.

Legs long. Profemur densely pubescent. Protibia pubescent. Protarsus with basal four tarsomeres tomentose, especially pubescent ventrally; apical tarsomere as long as preceding four tarsomeres combined, setose basally, for more than ½ length, glabrous apically (Fig. 125). Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, with few scattered setae, with small patch of golden setae at apex, setose patch only at very base of tibia; apex lacking excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta arising from fourth tarsomere; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa with distinct rounded projection posteriorly. Metatrochanter globose, with distinct posterior face (Fig. 133). Metafemur densely pubescent. Metatibia pubescent for entire length (Fig. 125). Apical metatarsomere glabrous on apical half (Fig. 125).

Abdomen densely pubescent, with five ventrites; ventrites constricted medially. First ventrite not excavated for reception of folded hind legs (Fig. 129). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 1.1mm long (Fig. 124). Aedeagus slender and strongly curved to apex. Parameres fused, pointed, with extended apex in lateral aspect.

Female. Length 3.9 mm; width 2.4 mm. Externally similar to male, females generally larger than males; abdominal ventrites of female not constricted medially; apical abdominal ventrite pointed (Fig. 129).

Intraspecific Variation. This species varies considerably in size, ranging from 2.2–3.9 mm long and 1.1–2.4 mm wide. Additionally, specimens vary slightly in color – from light reddish-brown to dark reddish-brown, specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease. Specimens also vary a surprising amount in body shape, with some specimens having a stronger wedge shape than others, and pronotal lateral borders with varying degrees of convergence.

Habitat and Distribution. *Auritrochus laticeps* is known from throughout the south-central United States and into northern Mexico (Fig. 24) At Turner Falls, Oklahoma, USA, the adults of *Autritrochus luteus* can be found from May-September in fast-flowing streams and rivers that are rich in calcium and often exhibit travertine or tufa deposits (Fig. 134). Adults are rapid fliers and will enter and exit the water with great ease – they are covered in a dense mat of hairs, which forms a hygrophobic coat, allowing them breathe underwater and to enter and exit the water without getting stuck in the surface tension (Figs. 135, 136, & AURLUT21). The beetles can be found congregating on the downstream sides of rocks, where they mate and presumably feed by scraping the periphyton on the rocks. In western Texas, imagoes of *A. luteus* have been found clinging to water-splashed mosses in a fast flowing stream through a road culvert that was located just below an impoundment (Figs. 137–139). These observations suggest that *A. luteus* is not truly aquatic, but inhabits the zone just at the waters edge.

Brown (1987) notes that the adults of this species may remain submerged for enough time to develop encrustations of calcium, much like those of aged *Stenelmis* (Elmidae) specimens. The closely related species, *Auritrochus arizonensis* Brown and Murvosh, 1970 and *Auritrochus luteus* LeConte,1852, have been reported from similar habitats in Arizona and Oklahoma, respectively (Brown and Murvosh 1970, Reisen 1977). The bedrock in these habitats is almost always limestone and travertine deposits are common (Fig. 136). Additionally, Brown (1987) has observed females of *L. luteus* grazing on algae and ovipositing in the travertine.

Larvae burrow into the travertine deposits, forming tracks through flaking travertine. Interestingly, at Turner Falls, Oklahoma, the larvae were found only in areas where brown algae and periphyton were plentiful (Fig. 140). Larvae may leave water to pupate, forming pupal cells in travertine or rotting wood. Adults are attracted to lights.

***Auritrochus shepardi* Maier & Short n. sp.**

(Figs. 142–149)

Type Material. Holotype male: "MEXICO: Querétaro; El Plátano; 10 VII 2000 1225 m; Arroyo El Plátano" "William D.; Shepard, leg." "PHOTO VOUCHER; PV_____; Short Lab – KU NHM [Green Label]" "CReAC001109; Aquatic Beetle Database" "Lutrochus; MX sp. B; W.D. Shepard" "HOLOTYPE; Auritrochus shepardi; des. Maier & Short 2016 [Red Label]" Holotype deposited in CNIN (Figs. 148 & 149). **Paratypes** (3): Same Data as Holotype (3 specimens EMEC). Same data as holotype, except collector "C.B. Barr" (10 specimens EMEC). "MEXICO: Querétaro; Ayutla; 14 VII 2000; Rio Ayutla" "William; Shepard, leg." "Lutrochus; Mexican sp. B." (4 specimens EMEC). "MEXICO: Querétaro, Sierra; Gorda Biosphere Reserve;

Rio Verdito N Neblinas; 21˚ 15.6' N, 99˚ 03.3' W; 12-VII-2000, C.B. Barr" (10 specimens EMEC, 2 specimens CNIN). Same data as previous 12 paratypes, except collector "W.D. Shepard" (6 specimens EMEC).

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Auritrochus shepardi* is not externally distinct from other species of *Auritrochus*, but can be distinguished from other species of *Auritrochus* by the distinctive male genitalia. The parameres of *A. shepardi* are elongate distally (Fig. 145). This species is also generally larger than other species of Auritrochus (Length 3.0–4.5 mm). It is restricted in range to the karstic areas near Queréotaro and San Luis Potosí States of Mexico.

Description. HOLOTYPE MALE. – Length 3.6 mm; width 2.3 mm. Body strongly wedge-shaped and strongly convex, brown to black with a golden to greenish sheen, densely pubescent; clothed dense, long, recumbent, golden setae (Figs. 142–144).

Head broad, nearly as broad as pronotum, frons flattened, weakly grooved beneath eye for reception of antenna. Eye rounded, large, with short, golden interfacetal setae; eyes strongly projecting from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown and testaceous at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin strongly curved, with brush of long setae apically, setae not reaching apex of labrum. Apical margin of labrum sinuate, with apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with dense, short, golden setae. Mandibles large, dark brown, sickle-shaped; apex of manidible with one broad, flattened tooth. Maxilla with 4-segmented palpus, apical palpomere sub-cylindrical, but expanded at apex, about as wide as long, rounded at apex. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, more than two times as wide as long at base, strongly bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 144). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum extremely convex (Fig. 142). Scutellum triangular, a little wider than long. Hypomeron excavate posteriorly to accommodate femur.

Elytron pubescent, dark brown with metallic gold sheen; without sutural striae; humerus strongly protuberant (Fig. 142). Lateral edge with distinct bead (Fig. 144), epipleuron not expanded, not appearing broad in ventral aspect (Fig. 143). Elytral apex acute (Fig. 142).

Prosternum transverse, approximately twice as wide as long; strongly deflexed to accommodate withdrawn head, with strong transverse fold anteriorly; anterior edge with strong bead (Fig. 143). Prosternal process about as wide as long, lacking bead laterally, rounded to obtuse posteriorly (Fig. 143), lateral edges strongly divergent. Mesoventrite pubescent, lacking glabrous patch (Fig. 143). Metaventrite with metafemoral lines convergent with katepisternal suture, lacking distinct mesotarsal rests (Fig. 143). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly entire length of metacoxae.

Legs long. Profemur densely pubescent. Protibia pubescent along entire length. Protarsus with basal four tarsomeres tomentose, especially pubescent ventrally; apical tarsomere as long as preceding four tarsomeres combined, setose to basal quarter, glabrous apically (Fig. 147). Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, except with distinct longitudinal row of sparse setae on lateral face; apex lacking excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta

arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with distinct rounded projection posteriorly. Metatrochanter globose, lacking hook-like posterior extension proximally (Fig. 143). Metafemur densely pubescent. Metatibia pubescent for entire length (Fig. 147). Metatarsus entirely glabrous (Fig. 147).

Abdomen densely pubescent, with five ventrites; ventrites constricted medially. First ventrite very shallowly excavated for reception of folded hind legs (Fig. 143). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 1.5mm long (Fig. 145). Aedeagus slender and curved evenly to apex. Parameres fused, pointed, with extended apex in lateral aspect.

Female. Length 4.5 mm; width 2.6 mm. Externally similar to male, females generally larger than males; abdominal ventrites of female not constricted medially; apical abdominal ventrite pointed (Fig. 80).

Intraspecific Variation. This species varies considerably in size, ranging from 3.0–4.5 mm long and 1.7–2.6 mm wide. Additionally, specimens vary slightly in color – from light gold to dark bronze, specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease. Specimens also vary a surprising amount in body shape, with some specimens having a stronger wedge shape than others, and pronotal lateral borders with varying degrees of convergence.

Habitat and Distribution. This species is found throughout the karstic areas in central Mexico, in and around the Queretaro and San Luis Potosi states (Fig. 25).

Etymology. This species is named in honor of the collector of the type series for this species, William D. Shepard, of the Essig Museum of Entomology.

***Berotrochus* Maier & Short**

Type Species *Berotrochus geniculatus* (Chevrolat, 1894)

Included Species. This is a monotypic genus, including only the type species.

Diagnosis. This genus is distinct, distinguished from all other described Lutrochidae by the following combination of characters: body form nearly parallel-sided (Fig. 150); antennae reaching past half-way down pronotum (Fig. 150); head with two rugose patches at occiput; mesotibiae with excavation for reception of mesotarsi (Fig. 162); mesotibia of female with ventral tomentose strip; parameres of male genitalia immovably fused to tegmen (Fig. 161).

Redescription. Body length 3.0–4.9 mm and body width 1.3–2.6 mm. Body ovate, weakly parallel-sided, dark brown to black, densely pubescent; clothed with short fine, recumbent setae (Fig. 150).

Head broadly rounded, deflexed ventrally, weakly grooved beneath eye for reception of antenna. Eye rounded, small with short golden interfacetal setae; eyes slightly projecting from outline of head. Antenna long, reaching nearly halfway down length of pronotum (Fig. 150), clothed with short, golden setae. Mouth hypognathus. Frontoclypeal suture indistinct. Clypeal margin straight, evenly clothed with golden setae (Fig. 159). Labrum clothed with recumbent golden setae, lacking transverse row of long setae at midline (Fig. 159). Mandible large, dark brown, blunt, lacking distinct teeth (Fig. 157). Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular, greatly expanded at apex (Fig. 156). Labial palpus 3-segmented; apical palpomere cylindrical, with field of sensillae at apex (Fig. 160).

Pronotum pubescent, roughly 2.1 times as wide as long at base, weakly bisinuate at base (Fig. 150); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct

bead, explanate laterally base (Fig. 151). Posterior margin only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum shallowly convex(Fig. 150). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur(Fig. 151).

Elytron pubescent, dark brown to black, widest in anterior quarter. Elytron shallowly convex, weakly parallel-sided; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent setae; humerus slightly protuberant (Fig. 150). Lateral edge with distict bead; epipleuron appearing narrow in ventral aspect. Elytral apex rounded to very slightly acuminate.

Prosternum transverse approximately twice as wide as long, explanate anteriorly to accommodate head; prosternal process sharply pointed. Metaventrite entirely pubescent; metafemoral lines extending nearly to the katepisternal suture, with distinct mesotarsal rests (Fig. 163). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 151).

Legs long and slender. Profemur densely pubescent, profemur entirely pubescent (Fig. 152). Protarsus with all tarsomeres tomentose. Mesofemur densely pubescent. Mesotibia entirely glabrous (in females with tomentose patch ventrally at apex), mesotibia smooth, not expanded, with apex excavated for reception of mesotarsus (Fig. 162). Mesotarsus glabrous (Fig. 152). Metatrochanter subrectangular (Fig. 161). Metafemur densely pubescent. Metatibia entirely tomentose, except for small bare patch at apex.Metatarsus with first four tarsomeres tomentose, apical tarsomere glabrous in apical ¾ (Fig. 152).

Abdomen entirely pubescent, with five ventrites, ventrites not constricted medially (Fig. 164). Metacoxal rests on first ventrite extending two thirds of the way to second ventrite. First

ventrite barely excavated for reception of hind legs. Apical ventrite of male shallowly notched(Fig. 164).

Male genitalia as illustrated, parameres blunt and immovably fused to basal piece (Fig. 153). Aedeagus broad, slightly curved.

Etymology. The generic name *Berotrochus* is derived from the Latin *Bero-* for "ocean nymph," referring to its distribution on the oceanic islands of Cuba and Hispaniola, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. The genus *Berotrochus* is restricted to the Greater Antilles, and represents the only Lutrochidae in the northern part of the West Indies. This lineage is unique in that it shares many of its morphological features with *Lutrochus*, from the Southern Hemisphere, and it shares its habits of living in travertine-depositing streams with *Auritrochus* in North America. Because of this, *B. geniculatus* represents a key taxon for understanding the transition between wood-boring to travertine-boring lifestyles. The larval habits are unknown, though the few specimens that have been collected share several key characters with larvae from *Auritrochus*.

Comparative Notes. Morphologically, *Berotrochus* is most similar to the *Lutrochus* from Central and South America. It shares the following characters with that genus: mesotibia with excavation, dorsal surface covered in fine, golden setae, mandibles short, securiform. It differs, though, in significant ways, including the long antennae, vestiture of the female mesotibiae, the structure of the male genitalia, and its distinctive habitat preferences. *Berotrochus* has two distinct rugose patches on the posterior face of the head, just anterior to the occiput. It shares this distinct character with *Andotrochus* and it is not seen anywhere else in the Lutrochidae or Byrrhoidea.

***Berotrochus geniculatus* (Chevrolat, 1894)**

Lutrochus geniculatus Chevrolat, 1894

(Figs. 150–169)

Type Material. *Lutrochus geniculatus:* Seven syntypes in NMHN. **Lectotype (here designated)**: [Card mounted. Card with "LT"] "Cuba, C^{n} Chevrol [green label, handwritten]" "Museum Paris;1917;Coll. Grouvelle [green label, printed]" "LECTOTYPE; *Lutrochus geniculatus*; Chevrolat, 1864; des. C. A. Maier 2015 [yellow label, printed]". **Paralectotypes (six paralectotypes, here designated)**: [Card Mounted. Card with "PLT"] "Cuba, C^{n} Chevrol [green label, handwritten]" "Museum Paris;1917;Coll. Grouvelle [green label, printed]" "PARALECTOTYPE; *Lutrochus geniculatus*; Chevrolat, 1864; des. C. A. Maier 2015 [sky blue label, printed]" [2 specimens, on same card as Lectotype]. [Card Mounted. Card with "PLT"] "Parnidae; gen. et spec.; nov.; Cuba; [reverse] Lutochrus geniculatus Chev. Cuba [illegible, see Fig. 168][weathered paper, handwritten, cursive]" "Museum Paris;1917;Coll. Grouvelle [green label, printed]" "PARALECTOTYPE; *Lutrochus geniculatus*; Chevrolat, 1864; des. C. A. Maier 2015 [sky blue label, printed]" [4 specimens, on same card].

Other Material Examined. See Appendix V for complete list.

Diagnosis. See generic diagnostic characters.

Description. LECTOTYPE MALE. Length 4.7 mm; width 2.8 mm. Body weakly parallel-sided and weakly convex, dark brown to black, densely pubescent; clothed with short, fine, recumbent golden hairs (Fig. 150).

Head broad, broadly rounded, with slight indentation on frons, weakly grooved beneath eye for reception of antenna. Eye rounded, medium-sized, with short, golden interfacetal setae; eyes slightly projecting from the outline of head (Fig. 150). Antenna long, reaching slightly past

halfway point of pronotum, apical nine antennomeres short, dark brown and only weakly clavate, clothed with short golden setae (Fig. 155). Frontoclypeal suture indistinct. Clypeal margin weakly curved, with sparse brush of short setae apically. Apical margin of labrum broadly arcuate, covered in sparse, recumbent golden setae, lateral setae twice as long as medial setae. Mandibles large, dark brown, blunt, dull; apex of mandible with very blunt teeth, if any; prostheca with proximal field of papilliform sensillae and a longitudinal comb of short, stout setae (Fig. 157). Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, strongly sinuate at apex, with field of small sensillae at apex (Fig. 156); galea with dense apical brush of setae lateral setae two times as long as medial setae; lacinia slightly shorter and smaller than galea or palpus, with dense brush of curved setae on inner margin (Fig. 156). Labial palpus 3-segmented; apical palpomere fusiform, with distinct patch of sensillae at apex (Fig. 160).

Pronotum pubescent, two times as wide as long at base, lateral edges nearly parallel-sided bisinuate at base (Fig. 150). Lateral edge of pronotum with distinct bead, explanate apically (Fig. 152). Posterior margin only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum broadly convex. Scutellum triangular, about as wide as long (Fig. 46). Hypomeron excavate posteriorly to accommodate femur (Fig. 151).

Elytron pubescent, dark brown, with dull sheen, widest in basal quarter (Fig. 150). Elytron broadly convex, lacking any evidence of distinct puncture rows, completely covered with fine punctation; elytral surface covered with dense, golden, recumbent setae; humerus only barely protuberant (Fig. 150). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 151). Elytral apex broadly rounded.

Prosternum transverse approximately two times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide

as long, with bead laterally, acutely angled posteriorly. Mesoventrite completely pubescent, lacking distinct, round glabrous patch medially. Metaventrite with prominent mesocoxal rests, with distinct recesses to accommodate mesotarsi (Fig. 163), Mesoventral lines very close to katepisternal suture. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender, only weakly expanded. Profemur densely pubescent. Protibia entirely pubescent. Protarsus with all tarsomeres tomentose, except for small glabrous patch dorsally at distal end of apical tarsomere; apical tarsomere 1.5 times as long as preceding four tarsomeres combined (Fig. 152). Mesocoxa with tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia completely glabrous dorsally, with small, longitudinal patch of golden setae ventrally, dorsally with four long, erect setae; apex with excavation laterally for reception of tarsus (Fig. 162). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere 1.2x as long as preceding four tarsomeres combined (Fig. 162). Metatrochanter subrectangular, without distinct posterior extensions. Metafemur densely pubescent. Metatibia entirely pubescent. Metatarsus with basal four tarsomeres pubescent; apical metatarsomere pubescent in basal quarter , with apical tarsomere as long as previous four combined (Fig. 152, 161).

Abdomen entirely pubescent, with five ventrites, ventrites not constricted medially (Fig. 164). Metacoxal rests on first ventrite extending two thirds of the way to second ventrite. Abdominal ventrites only barely constricted medially, roughly same longitudinal length across entire width of body. Apical ventrite with shallowly emarginate apically.

Genitalia as illustrated, basal piece + parameres 1.6 mm long. Aedeagus slender and curved, becoming more curved at tapered tip (Fig. 168). Parameres fused, pointed, with distinct lobes interiorly subapically.

Female.

Intraspecific Variation. This species varies considerably in size, ranging from 3.0–4.9 mm in length and 1.3–2.6 mm in width. Additionally, specimens vary slightly in color and luster – from dark brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease, giving the appearance of being darker or lighter.

Habitat and Distribution. *Berotrochus geniculatus* is uncommonly collected and is restricted to karst landscapes with travertine-depositing streams on the Greater Antillean islands of Hispaniola and Cuba (Spangler et al. 2001) (Fig. 26). This species is extremely uncommon in collections, with only 80 specimens known in collections around the world. The lack of collection is due to a combination of factors: 1) the specialized microhabitat in which *B. geniculatus* lives, and lack of knowledge among general collectors of these microhabitats, 2) the politically and economically isolated nature of the countries in its range, and 3) the unique habitat requirements of the species, as it is only found in travertine streams.

On Cuba, *B. geniculatus* is relatively widespread, found in the mountainous, karstic regions surrounding Santiago de Cuba, in thesoutheastern portion of the island and in the Trinidad Mountains, in the central region. The habitat in these localities bears striking resemblance to the travertine streams of Central Oklahoma and Texas, where species of *Auritrochus* are common.

On Hispaniola, *B. geniculatus* is far less common. A single specimen (MCZ), collected by P.J. Darlington in 1924, remained the only representative of the species known from the island for nearly 100 years (Darlington, 1936). The specimen was collected from Massif La Hotte, a major biodiversity hot spot on the Tiburon Peninsula in Haiti. It was then hypothesized by myself and colleagues in the Czech Republic that if it occurred in Haiti that it is widespread in karst regions throughout Hispaniola. In summer of 2014, a team of scientists (M. Fikacek, M.L. Gimmel, A. Deler-Henandez) surveyed the Dominican Republic, using methods specifically targeting Lutrochidae, and did not find any specimens.

Concurrently, University of Kansas researchers D. Baker and D. Huggins, in their surveys of aquatic habitats in the area surrounding Les Cayes, Haiti, attempted to collect Lutrochidae on several occasions. Finally, in March 2014, one specimen was collected at Rivière Glace, near the village of Duchity.

This represents the first modern-day observation of *B. geniculatus* in its native habitat on Hispaniola. Specimens were collected in a Riviere Glace, a medium-sized river with an open canopy, which flows off the northern slope of Pic Macaya on Massif La Hotte. At time of collection (23 March 2015), the water quality here was excellent, with high DO (11.54mg/L), low turbidity, and low embeddedness of the benthic substrate. It also displays heavy travertine deposition and supports the growth of ample filamentous green algae. This stream is a rarity in Haiti, and is one of few remaining pristine water bodies among hundreds of heavily anthropogenically influenced streams and rivers. Unfortunately, the only known habitat for *B. geniculatus* on Hispaniola is now threatened by development and road construction.

Adults appear to be active all year round throughout their range.

Notes. This species represents a unique lineage among Lutrochidae and study of its biology and evolution is pivotal to understanding the ecological and life-history transition between travertine and a life boring into wood, as they are morphologically very similar to *Lutrochus* species, but have the travertine-loving habits of *Auritrochus* species. Additionally, as a West Indian endemic, the species is of biogeographic importance to understanding past diversification patterns of the lineage.

Additionally, the type specimen of this species was surprisingly difficult to locate. In the original publication, Chevrolat described "Lutochrus geniculatus" from "Cuba" in a series of specimens in his personal collection, "Je possède plusieurs exemplaires de cette espèce [I own several copies of this species]". A series of speciemens deposited in the Grouvelle collection at MNHN, Paris, France, have labels that indicate "Cuba Cn Chevrol" and "Parnidae, gen. et sp. nov" and are most likely the syntype series of this species, though they do not bear a type label. An intact specimen from this series was chosen to be designated the Lectotype, and the rest are designated paralectotypes.

Lutrochus Erichson, 1847

Type Species

Lutrochus pilula Erichson, 1847

Diagnosis. This genus is distinct, but most closely resembles *Berotrochus* in size and vestiture of legs, and possesses the following suite of characters which separate it from all other genera: body form broadly ovate to slightly wedge-shaped (Figs. 170 & 329); antennae short, reaching no further than half-way down pronotum (Figs. 265 & 313); head lacking two rugose patches at

occiput; mesotibiae with excavation for reception of mesotarsi (Fig. 182); mesotibia of completely glabrous (Figs. 170 & 271); parameres of male genitalia broadly joined to tegmen (Fig. 186). Specimens of Lutrochus are also significantly larger than members of other genera, ranging in size from 4.0 mm to 6.6 mm.

Redescription. Body length 4.0–6.6 mm and body width 2.1–3.6 mm. Body ovate to wedge-shaped, reddish-brown to black, densely pubescent; completely clothed with setae (Fig. 304).

Head broadly rounded, deflexed ventrally, grooved beneath eye for reception of antenna. Eye rounded, with short golden interfacetal setae; eyes slightly projecting to smooth within outline of head. Antenna short to long, ranging from barely reaching anterior border of pronotum to reaching no further than half-way down pronotum (Figs. 265 & 313), clothed with short, golden setae. Mouth hypognathus. Frontoclypeal suture indistinct. Clypeal margin straight, clothed with setae (Fig. 351). Labrum evenly clothed with recumbent setae, lacking transverse row of long setae at midline (Fig. 351). Mandible large, stout, dark brown, falciform, with distinct teeth apically (Fig. 352). Maxilla with 4-segmented palpus, apical palpomere flattened and rounded to triangular, greatly expanded at apex (Figs. 353 & 289). Labial palpus 3-segmented; apical palpomere cylindrical, with field of sensillae at apex (Fig. 179).

Pronotum pubescent, weakly bisinuate at base (Fig. 170); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, not explanate to slightly explanate laterally at base (Fig. 171 & 362). Posterior margin straight or only shallowly excavate to receive anterior margin of scutellum. Disc of pronotum convex (Fig. 267). Scutellum triangular. Hypomeron excavate posteriorly to accommodate femur (Fig. 267).

Elytron pubescent, reddish brown to black, widest in anterior half. Elytron shallowly to strongly convex, sometimes weakly parallel-sided, but most often broadly rounded; elytral surface lacking distinct puncture rows, evenly covered with small punctures and dense recumbent or erect setae; humerus not to weakly protuberant (Figs. 304 & 339). Lateral edge with distict bead; epipleuron appearing narrow to wide in ventral aspect (Figs. 267 & 172). Elytral apex rounded to acuminate.

Prosternum transverse, approximately twice as wide as long, deflexed or not deflexed to accommodate head; prosternal process acute or rounded posteriorly. Metaventrite entirely pubescent; metafemoral lines broadly separated from the katepisternal suture, with distinct mesotarsal rests (Fig. 345). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 267).

Legs long and slender. Profemur densely pubescent, protibia entirely pubescent (Fig. 274). Protarsus with at least first four tarsomeres tomentose, apical tarsomere with varying degrees of setation. Mesofemur densely pubescent. Mesotibia entirely glabrous, mesotibia smooth, expanded or not, with apex excavated for reception of mesotarsus (Fig. 182). Mesotarsus glabrous (Fig. 274). Metatrochanter excavate for reception of metatibia, with strong to weak posterior projection (Fig. 183). Metafemur densely pubescent. Metatibia entirely tomentose, except for small bare patch at apex.Metatarsus entirely glabrous to entirely tomentose (Figs. 274 & 296).

Abdomen entirely pubescent, with five ventrites, ventrites not or weakly constricted medially (Fig. & 344 & 287). Metacoxal rests on first ventrite extending half to two thirds of the way to second ventrite. First ventrite excavated for reception of hind legs. Apical ventrite of male rounded to very shallowly notched (Fig. 344).

Male genitalia as illustrated, parameres blunt and broadly joined to basal piece (Fig. 186). Aedeagus straight to slightly curved. Parameres nearly completely fused.

Comparative Notes. Morphologically, *Lutrochus* is most similar to the *Berotrochus* from the Greater Antillies. It shares the following characters with that genus: mesotibia with excavation, dorsal surface covered in fine, golden setae, mandibles short, stout, securiform. It differs, though, in significant ways, including the shorter antennae, vestiture of the female mesotibiae, the structure of the male genitalia, and its distinctive habitat preferences.

Biology and Distribution. The genus Lutrochus is restricted to Central and South America, from Southern Mexico (Los Tuxtlas, Veracruz, Mexico) to Northern Argentina (Cordoba, Cordoba, Argentina). While typical habitat for other genera are restricted to calcium-rich regions, specimens of Lutrochus have been collected from streams with a wide range of geologic characters (including high-calcium streams), from carbonitic and gneissic, to granitic geology.

Adults stay submerged and are covered in a thick coat of hydrofuge hairs. Adults and larvae are found on decaying wood and in crevices, while only larvae found in carved galleries in interior portions of the wood (Ide et al 2005). In the case of *Lutrochus vestitus*, may also be found in water-splashed plant debris and root mats (Maier & Short, 2013). Larvae are long lived and have a simple, straight gut, which leads to production of large quantities of feces – similar to other wood boring aquatic insects (Valente Neto and Fonseca-Gessner 2011).

***Lutrochus acuminatus* Grouvelle, 1889**

(Figs. 170–189)

Type Material. *Lutrochus acuminatus:* Four syntypes in NMHN. **Lectotype** (Designated in Maier & Short 2013): [Point mounted. Point with "♂"] "Colonia Tovar; E. Simon 1.11.88" "Type" "[yellow label] LECTOTYPE; *Lutrochus acuminatus*; Grouvelle 1889; des. Maier & Short 2012". (Figs. 187 & 188) **Paralectotypes** (3, (Designated in Maier & Short 2013): [Point mounted. Point with "♀"] "Colonia Tovar; E. Simon 1.11.88" "Type". [2 specimens Card mounted] "Colonia Tovar; E. Simon 1.11.88" "Type" "[blue label] PARALECTOTYPE; *Lutrochus acuminatus*; Grouvelle 1889; des. Maier & Short 2012".

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Lutrochus acuminatus* can be distinguished from other species of *Lutrochus* by the explanate elytra, with the epipleuron appearing broad in ventral aspect (Figs. 171 & 172); its reddish-brown color; the strongly deflexed prosternum ventrally in anterior half (Fig. 175); and the strongly triangular apical maxillary palpomere (Figs. 174 & 177). This species is distinctive, and does not resemble any others found in Venezuela.

Redescription. LECTOTYPE MALE. – Length 3.0 mm; width 1.7 mm. Body ovate and strongly convex, reddish brown to medium brown, densely pubescent; clothed with two types of short, fine, golden hairs (Figs. 170 & 172). Dorsal setae erect and long mixed with dense, recumbent short setae. Short recumbent setae on pronotum facing anteriorly, short recumbent setae on elytra facing posteriorly, giving pronotum golden appearance in dorsal aspect (Fig. 170).

Head broad, broadly rounded, weakly grooved beneath eye for reception of antenna (Fig. 174). Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, clavate, medium brown and testaceous at apex, clothed with short, recumbent golden setae. Frontoclypeal suture indistinct. Clypeal margin curved slightly, with brush of long setae apically,

setae not reaching apex of labrum. Apical margin of labrum sinuate, with apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with dense , golden setae. Mandibles large, dark brown, falciform; apex of manidible with three short teeth (Fig. 181). Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, almost two times as wide as long, abruptly truncate at apex (Fig. 177). Labial palpus 3-segmented; apical palpomere cylindrical (Fig. 179).

Pronotum pubescent, two times as wide as long at base, bisinuate at base. Lateral edge of pronotum with distinct bead (Fig. 172). Posterior margin anterior to scutellum straight to slightly curved, without notch. Disc of pronotum broadly convex (Fig. 170). Scutellum triangular, a little wider than long. Hypomeron excavate posteriorly to accommodate femur.

Elytron pubsecent, reddish-brown, widest at midlength. Elytron broadly convex, with dense, small punctures, lacking puncture striae; humerus not protuberant (Fig. 170). Lateral edge with distinct bead (Fig. 172), epipleuron expanded, broad in ventral aspect (Fig. 171). Elytral apex rounded (Fig. 170).

Prosternum transverse, approximately 1.5 times as wide as long; strongly deflexed to accommodate withdrawn head, with strong transverse fold anteriorly; anterior edge with strong bead (Fig. 175). Prosternal process about 1.2 times as wide as long, lacking bead laterally, acuminate posteriorly (Fig. 175). Mesoventrite pubescent, lacking glabrous patch (Fig. 184). Metaventrite with metafemoral lines broadly separated from the katepisternal suture, lacking distinct mesotarsal rests. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly roughly halfway to metacoxae.

Legs short. Profemur densely pubescent. Protibia pubescent. Protarsus with apical four tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere

0.7 times as long as preceding four tarsomeres combined. Mesocoxa pubescent, lacking tuft of long golden setae basally. Mesofemur densely pubescent. Mesotibia completely glabrous, with few scattered setae, lacking small patch of golden setae at apex; apex with excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, lacking single long seta arising from fourth tarsomere; apical tarsomere 0.8 times as long as preceding four tarsomeres combined. Metatrochanter globose, with single short hook-like posterior extension proximally (Fig. 171). Metafemur densely pubescent. Metatibia pubescent for entire length, with distinct glabrous patch internally on apical ½ (Fig. 185). Metatarsus glabrous, with apical tarsomere 0.7 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites. First ventrite shallowly excavated for reception of folded hind legs (Fig. 171). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 1.9mm long (Fig. 186). Aedeagus slender and curved evenly to apex. Parameres fused, pointed, with extended apex in lateral aspect.

Female. Length 4.0 mm; width 2.0 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 3.0–4.3 mm long and 1.7–2.3 mm wide. Additionally, specimens vary slightly in color – from light reddish-brown to dark reddish-brown, specimens also have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. All newly collected specimens were found in small (<2 m wide), densely forested mountain streams at elevations over 1000 m. Most specimens were collected directly from submerged logs and woody debris (Fig. 189). The type locality and most additional collections were made in the Coastal Mountains of north-central Venezuela (Fig. 27). One additional collection was taken the adjacent northeastern extent of the Merida Andes.

Remarks. This species was previously the only named species in the family from Venezuela and also the only one recorded from Venezuela prior the publication of the Revision of the Lutrochidae of Venezuela (Maier & Short 2013).

***Lutrochus barrae* n. sp.**

(Figs. 190–197)

Type Material. Holotype male: "PANAMA: Chiriqui; Prov., Rio Colorado; at Volcan Rd., 5.6 rd. km NW Volcan; 25-VIII-2006, C.B. Barr" "08°49.913′ N 82°43.063′W; elevation 4101 ft" Holotype deposited in EMEC (Figs. 194 & 195). **Paratypes (34): PANAMA: Chiriqui Province:** Same locality data as holotype (12 specimens EMEC). "PANAMA: Chiriqui; Prov., Rio Colorado; trib at Volcan Rd.; ~4 rd. km NW Volcan; 25-VIII-2006, C.B. Barr" "08°48.405′ N 82°40.540′W; elevation 4388 ft" (2 specimens EMEC). **COSTA RICA: Puntarenas Province:** "COSTA RICA: Puntarenas; Prov., Las Cruces Biol.; Sta.S San Vito, Rio Jaba; 23-VI-2001, coll. C.B. Barr" "08°47'28"N 82°57'26"W; elevation 3199 ft" (14 specimens EMEC). "COSTA RICA: Puntarenas; Prov., Monteverde Biol.; Sta. E Santa Elena; Quebrada Moquina; 24 January 2000, coll. C.B. Barr" "10°18.55'N 84°48.16'W; elevation ca. 1500 m" (2 specimens EMEC). "COSTA RICA: Punta-;renas Prov., Rio Coton; near Las Alturus; 24-vi-2001, coll. C.B. Barr" "08°55'45"N 82°50'39"W; elevation 4080 ft" (2 specimens EMEC). "COSTA

RICA: Puntarenas Prov.; Rio Bella Vista; Las Alturas Biological; Station N of Alturas; 20-vi-2003, coll. C.B. Barr" "12°27.45'N 75°35.57'W; elevation 4360 ft" (1 specimen EMEC). **Alajuela Province:** "COSTA RICA: Alajuela; Prov. Rio Cariblanco at; Hwy 126, 8 km S San Miguel; 25-vi-2003, coll. C.B. Barr" "10°14.53'N 84°11.91'W; elevation 2580 ft" (1 specimen EMEC).

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species is most similar to others in the *Lutrochus montanus* species group. These are united by the completely bare hind tarsi and rectangular shape of the apex of the parameres in lateral aspect (Fig. 193). *Lutrochus barrae* **n. sp.** can be separated from *L. violaceus* by the completely densely pubescent apical protarsomere when viewed from above (Fig. 196), and from *L. montanus* by the apex of the parameres extended posteriorly when viewed laterally (Fig. 193). Additionally, the elytral humeri in *L. barrae* **n. sp.** protuberant from outline of the body, as opposed to smooth in *L. montanus*.

Description. HOLOTYPE MALE. – Length 4.5 mm; width 2.5 mm. Body slightly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, erect, dark bronze setae (Fig. 190).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna long, reaching slightly past anterior border of pronotum; antennomeres brunneous; antennomeres short and clavate, nearly serrate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with dense golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct

teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.25 times as wide as long at base, bisinuate at base (Fig. 190). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 192). Posterior margin of pronotum straight anterior to scutellum. Disc broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 192).

Elytron pubescent, clothed with dense, short, erect golden setae, medium brown, widest at anterior third. Elytron strongly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus protuberant, projecting from outline of body (Fig. 190). Lateral edge with distinct and weakly sinuate bead (Fig. 192). Elytron lacking faint sutural stria in apical third. Elytral apex rounded.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, rounded posteriorly (Fig. 191). Disc with weak carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, reddish brown. Procoxae transverse. Profemur densely pubescent, reddish brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, lacking dense patch of long golden setae apically (Fig. 197), excavate dorsally to receive protarsus, explanate laterally (Fig. 191). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four

tarsomeres combined, glabrous ventrally, densely pubescent nearly to apex dorsally (Fig. 197). Mesocoxa lacking tuft of short golden setae basally. Mesofemur with rounded margins, evenly pubescent, reddish brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with one distinct longitudinal carina (Fig. 192); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25x as long as preceding four tarsomeres combined. Metacoxa with two weak posterior projections. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae; apex glabrous, lacking fringe of setae. Metatarsus with all tarsomeres entirely glabrous, as in Fig 197, apical tarsomere as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 191). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation reaching nearly to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.8 mm long. Aedeagus slender and strongly curved at apex. Parameres fused, pointed, apex of fused parameres squarish in shape, apex nearly rectanglular, lobes not extended at apex (Fig. 193).

Female. Length 5.1 mm; width 3.1 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.3–5.1 mm long and 2.4–3.1 mm wide. Additionally, specimens vary slightly in color and luster from dark brown to black, and from slightly metallic to not metallic. Some specimens examined have

differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named "barrae" in honor of Cheryl Barr, who has made great contributions to the study of byrrhoid water beetles, and who collected a large series of this species.

Habitat and Distribution. Specimens of this species have been collected at high elevations (over 1200 m) throughout southern Central America, in Panama and Costa Rica (Fig. 28).

***Lutrochus browni* n. sp.**

(Figs. 198–205)

Type Material. Holotype: "BRAZIL: Para; 25 mi e. Marabá; 71/10/19" "Catalog No. OMNH-100894" "PHOTO VOUCHER; PV; Short Lab – KU NHM" "HOLOTYPE; *Lutrochus browni*; des. Maier & Short 2015." Holotype deposited in OMNH. (Figs. 202 & 203) This species is known only from the holotype specimen**.**

Diagnosis. This species most closely resembles *L. maldonadoi* Maier & Short, 2013 and *L. gimmeli* **n. sp.,** in that they share the characters of small size, oval apical maxillary palpomeres, and nearly complete vestiture of the apical metatarsomere. *Lutrochus browni* can be distinguished from the preceeding species by its distinctive tarsal setation – the pro- and metatarsi of *L. gimmeli* are completetly setose, but lack th distinctive bare patch (as seen in *L. gimmeli*) on the interior face. *Lutrochus browni* also has long dorsal pilosity and the setae on the elytra are arranged in faint rows, but not nearly as distinct as those of *L. gimmeli*.

Description. HOLOTYPE FEMALE. – Length 4.0 mm; width 2.1 mm. Body ovate and slightly convex, reddish brown, densely pubescent; clothed with long, fine, erect golden setae and shorter recumbent golden setae, dorsal setae arranged in faint longitudinal bands down elytra (Fig. 198).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with long, golden interfacetal setae; eyes slightly bulging from outline of head. Antenna long, reaching well past anterior border of pronotum; antennomeres 1–3 testaceous, antennomeres 4–11 light brunneous; antennomeres long and nearly serrate, clothed with short golden setae. Frotoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with short golden apical setal brush. Labrum clothed with sparse and short golden setae. Mandibles large, reddish brown, falciform; apex of mandible with 3 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and distinctly rounded. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, roughly two times as wide at base as long, bisinuate at base (Fig. 198). Lateral edge of pronotum with distinct bead, not explanate. Posterior margin of pronotum straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent silvery setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, medium brown, widest at anterior one third, posterior half gently narrowing; elytron clothed with dense, short, recumbent golden setae, and long, erect golden setae; setae arranged in faint longitudinal bands down length of elytron (Fig. 198). Elytron weakly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not protuberant (Fig. 198). Lateral edge of pronotum

with distinct and weakly sinuate bead (Fig. 200). Elytron lacking faint sutural stria in apical third. Elytral apex slightly acuminate.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, strongly acuminate posteriorly (Fig. 199). Disc with carinae to accommodate profemorae laterally. Metaventrite pubescent, disc fully clothed with setae. Epipleuron excavated to accommodate folded front and middle legs. Epipleuron narrowing posteriorly to metacoxae.

Legs long and slender, reddish-brown. Procoxae transverse. Profemur densely pubescent, reddish-brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, excavate dorsally to receive protarsus, protibia becoming more explanate distally (Fig. 201). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere shorter than preceding four tarsomeres combined, glabrous ventrally, pubescent to apex (Fig. 205). Mesocoxa lacking tuft of short golden setae basally. Mesofemur cylindrical, densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin slightly expanded, tibia roundish in cross-section, with distinct longitudinal carina; apex with excavation laterally for reception of mesotarsus. Mesotarsus testaceous, with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with two posterior projections (Fig. 199). Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia rounded in cross-section, entirely pubescent; with short, golden setae, apex lacking fringe of long setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere

pubescent to apex on exterior face, with distinct glabrous patch on interior face as in Fig. 248, shorter than previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 199). First ventrite shallowly excavate for reception of folded hind legs, excavation reaches nearly to posterior edge of ventrite. Apical ventrite broadly rounded, with shallow notch at apex of abdomen.

Genitalia as illustrated, basal piece + parameres 1.8 mm long. Aedeagus slender and only slightly curved. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes slightly extended at apex (Fig. 201).

Male. Males of this species are not known. Based on observations of closely related species, we expect that they are externally similar to female, males generally larger than females.

Intraspecific Variation. This is the only known specimen of the species. Based on observations of closely related species, individuals may vary slightly in color from dark brown to black, and may vary slightly in size and level of setation.

Etymology. This species is named "browni" after Dr. Harley P. Brown, a forerunner in the study of aquatic Byrrhoidea and the collector of the only known specimen.

Habitat and Distribution. This species is only known from a single locality in Pará State, Brazil (Fig. 29). Harley Brown did extensive collecting in the region, recovering this single specimen, along with several hundred *Lutrochus germari* Grouvelle.

Though not noted on the label, this specimen is likely from a tributary of the Rio Tocantins, a large, flat river which drains much of central Brazil.

Remarks. *Lutrochus browni* **n. sp.** shares its distinct body form with *L. maldonadoi* Maier & Short, 2013 of the Guiana Shield region of Venezuela and *L. gimmeli* **n. sp.**, from Amazonian Ecuador.

***Lutrochus cauraensis* Maier & Short, 2013**

(Figs. 206–217)

Type Material. Holotype male: "Venezuela – BO [Bolívar State]; Kanarakuni; Alto Caura 450m" "10.-13.9 1964; F.F. Yepez ; J. Bechyne lgt." Holotype deposited in MIZA. **Paratypes (6): VENEZUELA: Bolívar State:** Same locality data as holotype. Paratypes deposited in: 3 in MIZA, 2 in SEMC, and 1 in USNM.

Diagnosis. This species can be distinguished from all other *Lutrochus* species by the following combination of characters: large size (~4.5 mm), the mesotibia with apical excavation for protarsus, elytra not explanate, prosternum not deflexed in anterior half, apical protarsomere with a discrete pubescent patch in the basal third, with apical two-thirds glabrous (Fig. 209) and body without metallic sheen dorsally (Fig. 212).

Redescription. HOLOTYPE MALE. – Length 4.5 mm; width 2.2 mm. Body wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, recumbent golden setae (Fig. 212).

Head broad, broadly rounded, weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna short, reaching slightly past anterior border of pronotum, antennomeres short, dark brown and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum straight, with apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse golden setae. Mandibles large, dark brown, weakly falciform; apex of mandible blunt, lacking distinct teeth. Maxilla with 4-segmented

palpus, apical palpomere flattened and triangular, truncate at apex; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, 1.6 times as wide as long at base, bisinuate at base (Fig. 206). Lateral edge of pronotum with distinct bead, slightly explanate apically. Posterior margin straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, dark brown to medium brown, widest at anterior third. Elytron broadly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; elytron clothed with dense, short, recumbent golden setae; humerus not protuberant (Fig. 206). Lateral edge with distinct bead, bead weakly sinuate (Fig. 208). Elytron wih faint sutural stria in apical third. Elytral apex strongly acuminate.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, rounded posteriorly (Fig. 207). Mesoventrite pubescent, disc fully clothed with setae. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly to metacoxae.

Legs long and slender, reddish-brown. Profemur densely pubescent. Protibia entirely pubescent . Protarsus with proximal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous at base, pubsecent in apical two thirds (Fig. 209). Mesocoxa with tuft of short golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; apex with excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres entirely

glabrous; apical tarsomere 1.5 times as long as preceding four tarsomeres combined. Metatrochanter globose. Metafemur densely pubescent. Metatibia entirely pubescent, with short, golden setae (210). Metatarsus with proximal four tarsomeres entirely pubescent; apical tarsomere glabrous, as long as previous four combined (Fig. 211).

Abdomen densely pubescent, with five ventrites (Fig. 207). First abdominal ventrite shallowly excavated for reception of folded hind legs. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 2.4mm long. Aedeagus slender and curved, becoming more curved at tapered tip. Parameres fused, pointed, with short distinct lobes interiorly subapically (Fig. 214).

Female. Length 4.5 mm; width 2.6 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 4.5–5.0 mm long and 2.6–2.8 mm wide. Additionally, specimens vary slightly in color – from dark brown to black. I have also noted that specimens in the series examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named “cauraensis” after the type locality at Alto Caura, Bolívar State, Venezuela.

Habitat and Distribution. Specimens of this species are only known from a single collecting event at the type locality in Bolívar State, Venezuela (Fig. 30). They were collected at in the Alto Caura at an elevation of 450m. The habits and microhabitat preferences of this species are unknown.

Remarks. This species was not disarticulated for inclusion of internal morphological characters in phylogenetic study, as there are only 7 specimens of this species known.

***Lutrochus funkae* Maier & Short, 2014**

(Figs. 218–225)

Type Material. Holotype male: "GUYANA, Lethem (30kmSE); Moco Moco River; 3° 21′N, 59° 28′W; 6 Apr 1994; PJSpangler, coll[ectio]n #19" "Lutrochus; n. sp.?; funkae" "♀ 4.66 mm long; 2.53 mm wide" "HOLOTYPE; Lutrochus; funkae; P.J. Spangler" "♂ tail to YTS; to draw" "PHOTO VOUCHER; PV; Short Lab KU NHM" "USNM ENT; 00717778" Holotype deposited in USNM (Figs. 224 & 225).

Diagnosis. This species most closely resembles *L. maldonadoi* Maier & Short, 2013, but can be distinguished from this species by the lateral edge of the pronotum, which is not explanate (Fig. 223); the hind tarsi, which are only clothed with setae towards the base (as opposed to entirely pubescent in *L. maldonadoi*); and the distinctive male genitalia (Fig. 221). *Lutrochus funkae* can be distinguished from *L. wao* and *L. grenadensis* by the following combination of characters: pro-, meso-, and metathoracic legs two-toned, elytral epipleuron parallel-sided, and apical tarsomere testaceous apically, dark brown basally.

Redescription. HOLOTYPE MALE. – Length 3.9 mm; width 2.1 mm. Body ovate and slightly convex, dark brown to black, densely pubescent; clothed with short, fine, erect golden setae (Fig. 218).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes slightly bulging from outline of head. Antenna short, reaching slightly past anterior border of pronotum; antennomeres 1–3

testaceous, antennomeres 4–11 brunneous; antennomeres short and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae; labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 1.9 times as wide at base as long, bisinuate at base (Fig. 218). Lateral edge of pronotum with distinct bead, only very slightly explanate apically. Posterior margin straight anterior to scutellum. Disc broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, clothed in dense, short, recumbent golden setae, medium brown, widest at anterior half, posterior half gently rounded, coming to an rounded point at apex. Elytron shallowly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not at all protuberant (Fig. 218). Lateral edge with distinct and weakly sinuate bead (Fig. 220). Elytron lacking faint sutural stria in apical third. Elytral apex rounded, but slightly acuminate.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, acute posteriorly (Fig. 219). Disc of prosternum with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae. Epipleuron excavated to accommodate folded front and middle legs. Epipleuron nearly parallel-sided, extended posteriorly to metacoxae (Fig. 219).

Legs long and slender, dorsally testaceous, dark brown ventrally. Procoxae transverse. Profemur densely pubescent, reddish-brown dorsally, medium brown ventrally, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, excavate dorsally to receive protarsus, only slightly explanate. Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 223). Mesocoxa with tuft of short golden setae basally. Mesofemur fusiform, densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally, medium brown ventrally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin not expanded, tibia rounded in cross-section, lacking distinct longitudinal carinae; apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with single weak posterior projection. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, apex with distinct, distally-facing fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only in basal quarter as in Fig. 223, as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 219). First ventrite shallowly excavate for reception of folded hind legs, excavation reaches nearly to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.6 mm long. Aedeagus slender and only slightly curved, becoming more curved at base. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes not extended at apex (Fig. 221).

Female. The female of this species is unknown. Curiously, the holotype possesses a label that states: "♀ 4.66 mm long; 2.53 mm wide,"though Spangler's field notes indicate that this was the only specimen of *Lutrochus* collected on the expedition. Additionally, a thorough search of the Smithsonian's aquatic beetle collection did not turn up any more individuals.

Intraspecific Variation. This species is only known from a single specimen.

Etymology. This species is named "funkae" in honor of botanist Vicki Funk, who was instrumental in leading the Smithsonian expeditions to Guyana, on one of which this specimen was collected.

Habitat and Distribution. The single known specimen of the species was collected from leaf packs in the sandy and gravelly Moco Moco River in Guyana (Spangler, in litt., CReAC, 2015). The Moco Moco River is a small tributary of the Takutu River, near Lethem, Guyana, and lies just east of the border with Brazil (Fig. 31). This area, in the Rupununi savannah region, is mainly grassland habitat.

Remarks. This species was discovered as new and named by Paul J. Spangler, who passed away before describing it.

***Lutrochus germari* Grouvelle, 1889**

(Figs. 226-233)

Neolutrochus braziliensis Hinton 1939b: 180 [*nomen nudum*] **syn. nov.**

Type Material. Lectotype male: "Brasil; Theresopolis [green label, Grouvelle hand]" "Brazil; Theresopolis; (copied from original; label CAM 2015)" "Type" "CReAC003049" "LECTOTYPE; Lutrochus germari; Grouvelle, 1889; des. C.A. Maier 2013 [Yellow paper,

printed]" [point mounted]. Lectotype deposited in MNHN (Figs. 230 & 231). **Paralectotypes (13): BRAZIL: Rio de Janiero:** Same locality data as lectotype, card mounted on 6 pins. Paralectotypes deposited in MNHN.

Other Material Examined. See Appendix V for complete list.

Diagnosis. *Lutrochus germari* is most similar to *L. guarani,* which it is close to in geographic proximity and shares the character of the apical wing binding patch of the elytra (Fig. 261) and the pattern of setation of the tibiae and tarsi (Fig. 233). It can be distinguished from this species by its distinctive genitalia, which have fused parameres that are relatively wide at apex and not posteriorly produced (in lateral view) (Fig. 229).

Redescription. LECTOTYPE MALE. – Length 4.5 mm; width 2.5 mm. Body weakly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, erect, golden setae (Fig. 226).

Head broad, broadly rounded, strongly grooved beneath eye for reception of antenna. Eye rounded, large, with short, golden interfacetal setae; eyes projecting from outline of head. Antenna medium-length, reaching just past anterior border of pronotum; antennomeres testaceous; antennomeres short and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.5 times as wide as long at base, bisinuate at base (Fig. 226). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 228).

Posterior margin straight anterior to scutellum (Fig. 226). Disc broadly convex. Scutellum triangular, about as wide as long; clothed in recumbent slivery setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 228).

Elytron pubescent, clothed with dense, short, erect dark bronze setae, medium brown, widest at anterior third; setae arranged randomly across cuticle. Elytron convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus protuberant (Fig. 226). Lateral edge with distinct and weakly sinuate bead (Fig. 228). Elytron with sutural stria in distal third. Elytral apex rounded to slightly acuminate.

Prosternum transverse, two times as wide as long; anterior edge with strong bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acute posteriorly (Fig. 227). Disc smooth, with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally; transverse sulcus of metaventrite strongly bisinuate. Mesepisternum and epipleuron strongly excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, brown in color. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, lacking dense patch of long golden setae apically (Fig. 227), strongly expanded and excavate dorsally to receive protarsus, explanate laterally (Fig. 227). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 233). Mesocoxa lacking tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, medium brown. Mesotibia completely glabrous, with few scattered setae,

lacking small patch of short golden setae at apex; lateral margin greatly expanded, with two distinct longitudinal carinae (Fig. 227); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with weak posterior projections. Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent in basal one third, as in Fig. 233, as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 227). First abdominal ventrite strongly excavate for reception of folded hind legs, excavation only reaching two thirds of the way to posterior edge of ventrite. Apical ventrite rounded.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus slender and curved. Parameres fused, pointed, lobes not extended at apex (Fig. 229).

Intraspecific Variation. This species varies slightly in size, ranging from 4.4–5.6 mm long and 2.5–2.9 mm wide. Additionally, specimens vary slightly in color and luster from dark brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. This species is widely distributed throughout southern Brazil, and presumably into Paraguay, Argentina, and Uruguay, though no specimens have been collected there (Fig. 32).

The habitat and biology of *L. germari* is well documented in several recent publications. Ide et al. 2005 provide habitat information in southeastern Brazil and Valente Neto and Fonseca-

Gessner (2011) detailed the larval habits and life cycle, along with other wood-boring Dryopoidea, including *Stegoelmis* sp. (Coleoptera: Elmidae). Larvae develop in rotting wood in streams and as pupae, can be found in cells in rotting logs above the waterline (Costa et al. 1996).

Remarks. This type series of this species is made up of a series of syntypes, designated as such by the describer, Grouvelle. This series was located by Dr. Andrew Short (University of Kansas) in the Grouvelle collection at the MNHN. These specimens match the type locality in the original publication (Theresopolis, Brazil) and bear "Type" labels. Here, we designate a single male specimen, which has had its genitalia dissected and illustrated. This specimen originally shared a pin with two other specimens. We have removed it from the card (the card remains on the pin with a note) and it now bears lectotype labels. All other specimens in the series are now designated as Paralectotypes.

The species name "*Neolutrochus braziliensis*" was published in Hinton (1939b) with reference to Brown as the author. However, this species name never had a published description, and is therefore a *nomen nudum* and unavailable. Further, the specimens designated by Brown as "*Neolutrochus braziliensis*" were examined and found to be representatives of *Lutrochus germari*.

***Lutrochus gigas* Hinton, 1939a**

(Figs. 234–241)

Type Material. Holotype male: "Type [Round label, red border]" "Vilcanota; Peru" "Coll. Kraatz" "♂" "Bris.Mus.; 1963-766" "Lutrochus; gigas; '38 Hntn; Type" "Holotype; Lutrochus;

gigas; Hinton; conf[irmed]. Maier & Short 2015" "CreAC001117" Holotype deposited in BMNH. (Figs. 238 & 239) **Paratypes (2). Peru: Puno [?]:** Same locality data as Holotype (1 specimen, BMNH). "Co-type [Round label, yellow border]" "Peru; 902-8" "Lutrochus; gigas; in co[llection] Grouv[elle] [Grouvelle hand]" "Peru; Vilcanota" "CReAC003110" (1 specimen, BMNH).

Other Material Examined. See Appendix V for a complete list.

Diagnosis. *Lutrochus gigas* is unique among *Lutrochus* species, based on its "massive" size and distinctive male genitalia. The fused parameres are one fifth of the length of the basal piece, and are highly curved in lateral aspect, a character seen nowhere else in the genus (Fig. 237). This species also has an unusually sinuate posterior border of the pronotum, (Not represented accurately in Hinton's 1939 illustration of the species) (Fig. 234), and the elytral apex is strongly acuminate in both males and females (Fig. 240) At present, it is only known from a single drainage in Southeastern Peruvian Andes, near the border with Bolivia, in the Cordillera Vilcanota.

Redescription. HOLOTYPE MALE. – Length 6.4 mm; width 3.7 mm. Body strongly wedge-shaped and convex, dark brown to black, densely pubescent; clothed with short, fine, erect, dark bronze setae (Fig. 234).

Head broad, broadly rounded, grooved beneath eye for reception of antenna. Eye rounded, large, with short, golden interfacetal setae; eyes slightly projecting from outline of head. Antenna medium-length, reaching just past anterior border of pronotum; antennomeres testaceous; antennomeres short and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown,

falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, twice as wide as long at base, strongly bisinuate at base (Fig. 234). Lateral edge of pronotum with distinct bead, borders weakly explanate (Fig. 236). Posterior margin straight immediately anterior to scutellum (Fig. 234). Disc broadly convex. Scutellum triangular, about as wide as long; clothed in recumbent slivery setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 236).

Elytron pubescent, clothed with dense, short, erect dark bronze setae, medium brown, widest at anterior third; setae arranged randomly across cuticle. Elytron convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus protuberant; elytral border adjacent to humerus explanate (Fig. 234). Lateral edge with distinct and strongly sinuate bead (Fig. 236). Elytron lacking sutural stria. Elytral apex strongly acuminate (Fig. 240).

Prosternum transverse, two times as wide as long; anterior edge with strong bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acute posteriorly. Disc smooth, with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally; transverse sulcus of metaventrite strongly bisinuate (CHECK IN OTHERS!!). Mesepisternum and epipleuron strongly excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, reddish brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, with

dense patch of long golden setae apically (Fig. 236), only weakly excavate dorsally to receive protarsus, explanate laterally (Fig. 236). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 241). Mesocoxa lacking tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, medium brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with one distinct longitudinal carina (Fig. 236); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa lacking posterior projections. Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with tarsomeres entirely glabrous, as in Fig 241, 1.25 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 235). First abdominal ventrite strongly excavate for reception of folded hind legs, excavation only reaching two thirds of the way to posterior edge of ventrite. Apical ventrite rounded.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus slender and only slightly curved. Parameres fused, pointed, lobes curved and extended at apex (Fig. 237).

Female. Length 6.6 mm; width 3.6 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 6.4–6.6 mm long and 3.5–3.7 mm wide. Additionally, specimens vary slightly in color and luster from dark

brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. Despite extensive collecting effort by entomologists in Peru, this distinctive species is only found in a single drainage – the Urubamba River (called the Rio Vilcanota in the headwater region) (Fig. 33). Streams in this area are high grade alpine streams in the Cordillera Vilcanota, at roughly ~3000 m elevation (specimen labels do not indicate exact elevation at the locality where they were collected).

Remarks. Based on Hinton (1939a), the type of *Lutrochus gigas* should have been deposited at the Deutsches Entomologisches Institut in Senckenberg, Germany, however the holotype and two paratypes were found in the Natural History Museum, London. These three specimens bear Hinton's type labels and labels indicating that they were once part of the Kraatz collection, but also bear accession labels from the NHM, providing evidence that they were indeed accessioned. These have been returned to the NHM, London, to match accession records at that institution.

***Lutrochus gimmeli* Maier & Short n. sp.**

(Figs. 242–248)

Type Material. Holotype male: "ECUADOR: Oranella Prov.; Tiputini Biodiversity Stn.; 00° 38.2′ S 76° 08.9 ′ W; 4 Aug 2008 M. Gimmel; at large – by hand/sweep" "PHOTO VOUCHER; PV; Short Lab – KU NHM" "CREAC003060" Holotype found in material from LSAM, deposited in FMNH (Figs 246 & 247). This is a unique specimen, no paratypes exist.

Diagnosis. This species most closely resembles *L. maldonadoi* Maier & Short, 2013 and *L. browni* **n. sp.** *Lutrochus gimmeli* can be distinguished from the preceeding species by its distinctive tarsal setation – the pro- and metatarsi of *L. gimmeli* are completetly setose, but have a distinctive bare patch on the interior face. *Lutrochus gimmeli* also has long dorsal pilosity and the setae on the elytra are arranged in distinct rows.

Description. HOLOTYPE MALE. – Length 4.0 mm; width 2.1 mm. Body ovate and slightly convex, dark brown to black, densely pubescent; clothed with long, fine, erect golden setae and shorter recumbent golden setae, dorsal setae arranged in distinct longitudinal bands down elytra (Fig. 242).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with long, golden interfacetal setae; eyes bulging from outline of head. Antenna long, reaching well past anterior border of pronotum; antennomeres 1–3 testaceous, antennomeres 4–11 brunneous; antennomeres short and clavate, clothed with short golden setae. Frotoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 3 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 1.75 times as wide at base as long, bisinuate at base (Fig. 242). Lateral edge of pronotum with distinct bead, not explanate. Posterior margin of prontoum slightly emarginate anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent silvery setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, medium brown, widest at anterior one third, posterior half gently rounded ; elytron clothed with dense, short, recumbent golden setae, and long, erect golden setae; setae arranged in distinct longitudinal bands down length of elytron (Fig. 242). Elytron weakly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus slightly protuberant (Fig. 242). Lateral edge of pronotum with distinct and weakly sinuate bead (Fig. 244). Elytron lacking faint sutural stria in apical third. Elytral apex rounded.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, strongly acuminate posteriorly (Fig. 243). Disc with carinae to accommodate profemorae laterally. Metaventrite pubescent, disc fully clothed with setae. Epipleuron excavated to accommodate folded front and middle legs. Epipleuron narrowing posteriorly to metacoxae.

Legs long and slender, reddish-brown. Procoxae transverse. Profemur densely pubescent, reddish-brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, excavate dorsally to receive protarsus, protibia becoming more explanate distally. Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent to apex on exterior face, with distinct glabrous patch on interior face (Fig. 248). Mesocoxa lacking tuft of short golden setae basally. Mesofemur cylindrical, densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin slightly expanded, tibia flat in cross-section, with distinct longitudinal carinae; apex with excavation laterally for reception of

mesotarsus. Mesotarsus testaceous proximally and brunneus distally, with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with two posterior projections (Fig. 243). Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent; with short, golden setae, apex lacking fringe of long setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent to apex on exterior face, with distinct glabrous patch on interior face as in Fig. 248, as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 243). First ventrite shallowly excavate for reception of folded hind legs, excavation reaches nearly to posterior edge of ventrite. Apical ventrite broadly rounded, with shallow notch at apex of abdomen.

Genitalia as illustrated, basal piece + parameres 1.8 mm long. Aedeagus slender and only slightly curved. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes slightly extended at apex (Fig. 245).

Female. Females of this species are not known. Based on observations of closely related species, we expect that they are externally similar to male, females generally larger than males.

Intraspecific Variation. This is the only known specimen of the species. Based on observations of closely related species, individuals may vary slightly in color from dark brown to black, and may vary slightly in size and level of setation.

Etymology. This species is named “gimmeli” in honor of the collector of the only known specimen, Dr. Matthew L. Gimmel, of the Santa Barbara Natural History Museum.

Habitat and Distribution. This species is known only from the type locality at Tiputini Biodiversity Station in the Ecuadorian Amazon, just north of Rio Tiputini, a tributary to the

Napo River (Fig. 34). This site is composed of mostly primary non-flooded forests and the single specimen was collected while sweeping vegetation (M.L. Gimmel, pers. comm.).

***Lutrochus grenadensis* Maier & Short, 2014**

(Figs. 249–255)

Type Material. Holotype male: "Mont Plaisir R., Grenada; May 16, 1965 H. P. Brown" "Lutrochus ~~luteus~~; 22 a[dults] 1 l[arva]" "LABOULBENIALES; R.K. Benjamin; No. Ex." "OMNH-20661" Holotype deposited in OMNH (Figs. 253 & 254). **Paratypes (31):** **GRENADA: St. John:** Same locality data as holotype (21 specimens). "Concord Stream, Grenada; May 16, 1965 H. P. Brown" "Lutrochus; det. H.P. Brown" "LABOULBENIALES; R.K. Benjamin; No. Ex." [See *Remarks* for explanation] "OMNH 20660" (10 specimens, 1 disarticulated for phylogenetic study). "Little R., Gouyave; Grenada, West Indies; May 16, 1965 H. Brown" "Lutrochus; det. H. Brown" "PHOTO VOUCHER; PV; Short Lab KU NHM" "Catalog No.; 100892" Paratypes will be deposited in: 27 in OMNH, 3 in SEMC, and 1 in USNM.

Other Material Examined: "St. George's, Grenada; May 15, 1965 H. Brown" "Lutrochus ? 2; det. H. P. Brown" "LABOULBENIALES; R.K. Benjamin; No. Ex." "OMNH 20658"

Diagnosis. This species most closely resembles *L. maldonadoi* Maier & Short, 2013, but can be distinguished from this species by the lateral edge of the pronotum, which is not explanate (Fig. 3); the hind tarsi, which are only clothed with setae towards the base (as opposed to entirely pubescent in *L. maldonadoi*) (Fig. 255). *Lutrochus grenadensis* can be distinguished from *L. wao* and *L. funkae* by the following combination of characters: pro-, meso-, and metathoracic legs

entirely testaceous (Fig. 251), elytral epipleuron parallel-sided, and apical tarsomere testaceous, and distinctive male genitalia (Fig. 252).

Redescription. HOLOTYPE MALE. – Length 4.0 mm; width 2.1 mm. Body ovate and slightly convex, dark brown to black, densely pubescent; clothed with short, fine, erect golden setae (Fig. 249).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes slightly bulging from outline of head. Antenna short, reaching slightly past anterior border of pronotum; antennomeres 1–3 testaceous, antennomeres 4–11 brunneous; antennomeres short and clavate, clothed with short golden setae. Frotoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 3 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular. Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 1.8 times as wide at base as long, bisinuate at base (Fig. 249). Lateral edge of pronotum with distinct bead, not explanate. Posterior margin straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, medium brown, elytron clothed with dense, short, recumbent golden setae, widest at anterior one third, posterior half gently rounded. Elytron strongly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus slightly protuberant (Fig. 249). Lateral edge with distinct and weakly sinuate bead (Fig. 251). Elytron lacking faint sutural stria in apical third. Elytral apex rounded.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, rounded posteriorly (Fig. 250). Disc with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae. Epipleuron excavated to accommodate folded front and middle legs. Epipleuron narrowing posteriorly to metacoxae.

Legs long and slender, reddish-brown to testaceous. Procoxae transverse. Profemur densely pubescent, reddish-brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, excavate dorsally to receive protarsus, only slightly explanate. Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 255). Mesocoxa with tuft of short golden setae basally. Mesofemur fusiform, densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin not expanded, tibia rounded in cross-section, lacking distinct longitudinal carinae; apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with single weak posterior projection. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, apex with distinct, distally-facing fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only at base, as in Fig 10, as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 250). First ventrite shallowly excavate for reception of folded hind legs, excavation reaches nearly to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.8 mm long. Aedeagus slender and only slightly curved, becoming more curved at base. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes greatly extended at apex (Fig. 252).

Female. Length 4.0 mm; width 2.2 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 3.2–4.0 mm long and 2.0–2.2 mm wide. Additionally, specimens vary slightly in color from dark brown to black. We have also noted that specimens in the series examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named "grenadensis" after the type locality on the island of Grenada in the West Indies.

Habitat and Distribution. This species is widespread on the west coast of the island of Grenada in the West Indies. They are found in several coastal streams in St. John Parish, Mon Plaisir River, Concord Stream, and the Little River (Fig. 35). The exact habitat is not known.

Remarks. This species from Grenada marks the first known record of the family from the Lesser Antilles in the West Indies. While one other species, *Lutrochus geniculatus* Grouvelle, is known from the West Indies, its range includes only Cuba and Haiti on the island of Hispaniola. Morphologically, *L. grenadensis* bears similarity to several species from continental South America (*L. funkae*, *L. wao*, *L. maldonadoi*), but not to *L. geniculatus,* and therefore, is

likely more closely related to those species. Moreover, Grenada, with its geographic proximity to the coast of South America, has been documented to have continental affinities and shares many taxa with the mainland (Genoways et al. 2010). Given this new record, *Lutrochus* spp. are likely to be on Trinidad and Tobago as well.

Grenada is the furthest south of the Leeward Islands of the Lesser Antilles and is volcanic in origin (Earle 1923), therefore, lutrochids must have dispersed over ocean and this is likely not the result of a vicariance event. We can speculate as to the mode of dispersal to Grenada, with one of two modes likely – either by rafting in waterlogged wood as larvae, as other wood-boring beetles are wont to do (Peck 1996, 2001, Peck and Kukalová-Peck 1990), or through flight by winged adults.

Also worth noting is the label which states "LABOULBENIALES/ R.K. Benjamin/ No. Ex." Laboulbeniales is a group of ectoparasitic ascomycete fungi which live on the integument of insects and it includes many host-specific species (Weir and Hammond 1997). A thorough examination of the specimens showed no obvious thalli on the exoskeleton – presumably the specimens were removed by the Laboulbeniales specialist R.K. Benjamin and studied separately.

Only two specimens from the St. George's population are known from museum collections. These two specimens differ only slightly from the type series of *L. grenadensis*. These specimens, both male, were noted by Harley P. Brown as "Lutrochus ? 2" possibly indicating that they may be a second species from Grenada or, more likely, this was an annotation of the number of specimens collected at this site (this possibility was brought to my attention by one of the reviewers). Unfortunately, though, both specimens have the genitalia damaged, and oddly, in the exact same manner, with the tip broken off (*cf*. Maier & Short 2014,

Fig. 18) and so could not be definitively identified. I will refer to these specimens as *Lutrochus grenadensis*, however they are not included in the type series.

***Lutrochus guarani* Maier & Short n. sp.**

(Figs. 256–263)

Type Material. Holotype: "PARAGUAY: Central; Capiata; 17 VI 2006; WDS-A-1686 [reverse side]" "William D. Shepard, leg" "CreAC001096" "PHOTO VOUCHER; PV; Short Lab KU NHM" "HOLOTYPE; Lutrochus guarani; des. Maier & Short 2015" Holotype deposited in EMEC. (Figs. 260 & 263) **Paratypes (48). PARAGUAY: Alto Paraná Department:** "PARAGUAY: Dpto.Alto; Paraná v. sm. arroyo; 24 rd kmNE Yguazú; 5 rd. km SW Col. Laura; 21 Feb 2011, C.B. Barr" "25°17.988' S; 54°52.994' W; elevation ~226 m" (2 specimens EMEC). **Canindeyú Department:** "PARAGUAY: Canindeyú; 4.6 km W Cruce Curuguaty; 22 ii 2011 147 m; Arroyo Itandey; S24°30.859' W55°43.369'; WDS-A-1844 [reverse side]" "William D.; Shepard leg." (3 specimens EMEC). "PARAGUAY: Dpto. Canindeyú; Arroyo Itandey at Ruta 40; 4.6 km W Cruce Curuguaty; 22 Feb 2011, coll. C.B. Barr" "24°30.859' S 55°43.369' W; elevation ~147 m" (5 specimens EMEC). **Central Department:** Same locality data as Holotype (11 specimens, EMEC). **Cordillera Department:** "PARAGUAY: Cordillera; N of Caacupe; 27 vi 06; 280' Arroyo Ytu; WDS-A-1701 [reverse side]" "William D.; Shepard leg." (4 specimens EMEC). "PARAGUAY: Cordillera; 5 km E of Altos; 20 vi 2006; Tajý Cañada; WDS-A-1690 [reverse side]" "William D.; Shepard leg." (3 specimens EMEC). "PARAGUAY: Cordillera; 3.4 km S Atyrá; 20 vi 2006; unnamed stream; WDS-A-1691 [reverse side]" "William D.; Shepard leg." (3 specimens EMEC). "PARAGUAY: Cordillera; km 75.5 of road between; Atyrá and Caacupe 20 vi 06; unnamed stream; WDS-A-1692 [reverse side]"

"William D.; Shepard leg." (1 specimen EMEC). **Itapúa Department:** "PARAGUAY: Dpto. Itapúa; Arroyo Ypecurú at Ruta; Graneros del Sur ~17 rd km; NW jct. Ruta 6/Capt. Miranda; 19 Feb 2011, coll. C.B. Barr" "27°07.480' S; 55°55.326' W; elevation ~125 m" (3 specimens EMEC). "PARAGUAY: Dpto. Itapúa; Arroyo Curé-I or trib. 4.3; rd. km NW Nueva Alborada;; 20 Feb 2011, coll. C.B. Barr" "27°15.717' S; 55°39.278' W; elevation ~123 m" (1 specimen EMEC). **Paraguari Department:** "PARAGUAY: Paraguari; S of Sapucai; 21 vi 2006 550'; Arroyo Cuazú Cuá; WDS-A-1693 [reverse side]" "William D.; Shepard leg." (2 specimens EMEC). "PARAGUAY: Paraguari; P.N. Yvicui; 26 vi 2006 640'; Arroyo Mina; WDS-A-1700 [reverse side]" "William D.; Shepard leg." (2 specimens EMEC). "PARAGUAY: Paraguari Dept.; Ybycui (25 km SE); Ybycui National Park; 12-24 April 1980; P.J. Spangler et al." (3 specimens USNM). **San Pedro Department:** "PARAGUAY: Dpto. San Pedro; sm arroyo SE San Estanislao; 2.3 rd km W off Ruta 8; at 5 rd. km S of Tacuara; 25 Feb 2011, coll. C.B. Barr" "Defunct Balneario Piróy; 24°43.599' S; 56°20.954' W; elevation ~218 m" (3 specimens EMEC).

Diagnosis. *Lutrochus guarani* is most similar to *L. germari*, which it is close to in geographic proximity, and shares the character of the apical wing binding patch of the elytra (Fig. 261) and the pattern of setation of the tibiae and tarsi (Fig. 264). It can be distinguished from this species by its distinctive genitalia, which have fused parameres that are narrowed and posteriorly produced (Fig. 259).

Description. HOLOTYPE MALE. – Length 4.5 mm; width 2.5 mm. Body weakly wedge-shaped and convex, dark brown to black, densely pubescent; clothed with short, fine, erect, dark bronze setae (Fig. 256).

Head broad, broadly rounded, strongly grooved beneath eye for reception of antenna. Eye rounded, large, with short, golden interfacetal setae; eyes projecting from outline of head. Antenna long, reaching just past anterior border of pronotum; antennomeres testaceous; antennomeres short and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.25 times as wide as long at base, bisinuate at base (Fig. 256). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 258). Posterior margin straight anterior to scutellum (Fig. 256). Disc broadly convex. Scutellum triangular, about as wide as long; clothed in recumbent slivery setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 258).

Elytron pubescent, clothed with dense, short, erect dark bronze setae, medium brown, widest at anterior third; setae arranged randomly across cuticle. Elytron convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus slightly protuberant (Fig. 256). Lateral edge with distinct and weakly sinuate bead (Fig. 258). Elytron lacking sutural stria. Elytral apex rounded.

Prosternum transverse, two times as wide as long; anterior edge with strong bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acute posteriorly (Fig. 257). Disc smooth, with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae

laterally; transverse sulcus of metaventrite strongly bisinuate (Fig. 257). Mesepisternum and epipleuron strongly excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, reddish brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, lacking dense patch of long golden setae apically (Fig. 257), strongly expanded and excavate dorsally to receive protarsus, explanate laterally (Fig. 257). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 264). Mesocoxa lacking tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, medium brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with two distinct longitudinal carinae (Fig. 257); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa lacking posterior projections. Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent in basal one third, as in Fig 264, 1.25 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 257). First abdominal ventrite strongly excavate for reception of folded hind legs, excavation only reaching two thirds of the way to posterior edge of ventrite. Apical ventrite rounded.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus slender and curved. Parameres fused, pointed, lobes slightly extended at apex (Fig. 259).

Female. Length 4.7 mm; width 2.6 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.5–4.7 mm long and 2.5–2.6 mm wide. Additionally, specimens vary slightly in color and luster from dark brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named *Lutrochus guarani*, in honor of the Guarani people of Paraguay, where the species was first collected. This species was first noted as new and informally named by Dr. William Shepard.

Habitat and Distribution. This species is restricted to smaller streams in the Atlantic Forest of the Alto Paraná in southeastern Paraguay (Fig. 36). Most streams in this region drain into the Rio Parana.

***Lutrochus gustafsoni* Maier & Short, 2013**

(Figs. 265–276)

Type Material. [Published in error in Maier & Short 2013, this is actually the holotype of *L. maldonadoi* - **Holotype male:** "Venezuela Exp.;Culebra N. Duida; Territ. Amazonas; April 7-16 1950" "J. Maldonado; Capriles Coll." "USNM00768075" Holotype deposited in MIZA.] The correct holotype information for *L. gustafsoni* is: **Holotype female:** "Venezuela Exp.;Territ. Amazonas; Upper Cunucunuma; June 9, 1950" "J. Maldonado; Capriles Coll." "USNM00768071" Holotype deposited in MIZA.

Paratypes (2): VENEZUELA: Amazonas State: "Venezuela Exp.;Territ. Amazonas; Upper Cunucunuma; Apr. 28, 1950" "J. Maldonado; Capriles Coll." (1 specimen, USNM). "Venezuela Exp.;Territ. Amazonas; Upper Cunucunuma; Apr. 20, 1950" "J. Maldonado; Capriles Coll." (1 specimen, USNM). Paratypes deposited in: 1 in SEMC, 1 in USNM.

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species closely resembles *L. violaceus* and *L. cauraensis*, but can be distinguished from these and all other described Lutrochidae by its large size, short antennae, and the entirely glabrous apical protarsomere, which is least 1.5 times as long as previous four combined (Fig. 269). Also, the Brazilian species, *L. pilula* Erichson is the only other large (>4.5 mm) species with short antennae that barely reach the anterior margin on the pronotum and can be differentiated from *L. gustafsoni* by the former's entirely pubescent apical protarsomere.

Redescription. HOLOTYPE MALE.– Length 5.0 mm; width 2.9 mm. Body wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with distinctly short, fine, slightly recumbent golden hairs (Fig. 268).

Head broad, broadly rounded. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna very short, reaching only the anterior border of pronotum, antennomeres dark brown and clavate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae nearly as long as labrum. Apical margin of labrum sinuate, with short apical setal brush. Labrum clothed with sparse, golden setae. Mandibles large, dark brown, weakly falciform, robust; apex of manidible blunt, lacking distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex. Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, two times as wide as long at base, bisinuate at base (Fig. 265). Lateral edge of pronotum with distinct bead, broadly rounded. Posterior margin straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, dark brown to medium brown, widest at anterior third (Fig. 265). Elytron broadly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; elytron clothed with dense, very short, recumbent golden setae; humors not protuberant. Lateral edge with distinct bead, bead sinuate (Fig. 267); elytral epipleuron appearing narrow in ventral aspect (Fig. 266). Elytron with very weak sutural stria in apical fourth. Elytral apex broadly rounded (Fig. 265).

Prosternum transverse, approximately 1.8 times as wide as long; anterior edge with weak bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, obtusely angled posteriorly (Fig. 266). Mesoventrite pubescent, disc fully clothed with setae. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly to metacoxae.

Legs long and slender, dark brown. Profemur densely pubescent. Protibia entirely pubescent (Fig. 270). Protarsus with proximal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere 1.5 times as long as preceding four tarsomeres combined, entirely glabrous (Figs. 269 & 274). Mesocoxa with tuft of short golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; apex with excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres almost entirely glabrous, with small golden tufts of setae dorsally; apical tarsomere 1.5 times as long as

preceding four tarsomeres combined (Fig. 271). Metatrochanter globose. Metafemur densely pubescent. Metatibia pubescent to apical sixteenth, apical sixteenth glabrous. Metatarsus with proximal four tarsomeres entirely pubescent; apical tarsomere glabrous, 1.5 times as long as previous four combined (Fig. 272).

Abdomen densely pubescent, with five ventrites. First abdominal ventrite shallowly excavated for reception of folded hind legs. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + fused parameres 2.2mm long. Aedeagus slender and curved, becoming more curved at tapered tip. Parameres fused, pointed, with short, distinct lobes interiorly subapically (Fig. 273).

Female. Length 4.6 mm; width 2.6 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 4.6–5.0 mm long and 2.6–2.9 mm wide. Additionally, specimens vary slightly in color from dark brown to black. I have also noted that specimens in the series examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named for Grey Gustafson, a fellow aquatic coleopterist, who has collected many species of lutrochids in Venezuela

Habitat and Distribution. This species is restricted to Southern Venezuela on the Upper Orinoco River drainage. They have been collected at three localities from the upper Rio Cunucunuma in Amazonas State, Venezuela, north of Cerro Duida, on the Culebra savannah (Drake and Capriles 1952) and from the Upper Orinoco River, near the Isla de las Hormigas (Fig. 37). The habits and microhabitat preferences of this species are unknown.

Remarks. This species was not disarticulated for inclusion of internal morphological characters in phylogenetic study, as there are only 3 specimens of this species known. This species bears affinities to the Surinamese species *Lutrochus leeanneae*.

***Lutrochus leeanneae* Maier & Short, 2014**

(Figs. 277–285)

Type Material. Holotype: "SURINAME: Sipaliwini;2° 58' 38.316"N, 55° 23' 5.9928"W, 200 m; Camp 4 (low): Kasikasima; 24-iii-2012 ; leg. Short; UV light trap; SR12-0322-LT4" Holotype deposited in NZCS. (Figs. 281 & 282) **Paratypes (5). SURINAME: Sipaliwini:** "SURINAME: Sipaliwini;2° 58' 38.316"N, 55° 23' 5.9928"W, 200 m; Camp 4 (low): Kasikasima; 24-iii-2012 ; leg. Short; UV light trap; SR12-0322-LT4" (5 specimens, SEMC).

Diagnosis. This species is most similar to *L. gustafsoni* and *L. cauraensis*, two species which occur in southern Venezuela. These share the characters of the lateral margin of the mesotibia greatly expanded, with two distinct longitudinal carinae; and the metatarsi of all three species are completely glabrous. *Lutrochus leeanneae* can be distinguished from these two species by the presence of a dense patch of long golden setae apically on the protibia of the male (Fig. 283); and protarsi glabrous ventrally, pubescent nearly to apex dorsally (Fig. 283).

Redescription. HOLOTYPE MALE. – Length 4.5 mm; width 2.5 mm. Body slightly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, recumbent, dark bronze setae (Fig. 277).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna short, reaching slightly past anterior border of pronotum; antennomeres I-III testaceous

below, brunneous above, antennoeres IV-XI brunneous; antennomeres short and clavate, nearly serrate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.0 times as wide as long at base, bisinuate at base (Fig. 277). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 278). Posterior margin straight anterior to scutellum. Disc broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 279).

Elytron pubescent, clothed with dense, short, recumbent dark bronze setae, medium brown, widest at anterior third. Elytron strongly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus protuberant (Fig. 277). Lateral edge with distinct and weakly sinuate bead (Fig. 279). Elytron lacking faint sutural stria in apical third. Elytral apex rounded and slightly acuminate.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acute posteriorly (Fig. 278). Disc smooth, lacking carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, dark brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, with dense patch of long golden setae apically (Fig. 283), excavate dorsally to receive protarsus, explanate laterally (Fig. 285). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere 1.25 times as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 283). Mesocoxa with tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally, medium brown ventrally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with two distinct longitudinal carinae (Fig. 284); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa with two weak posterior projections. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae; apex glabrous, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only at base, as in Fig 283, 1.25 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 278). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation only reaching halfway to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus very slender and only slightly curved. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes not extended at apex (Fig. 280).

Female. Length 4.7 mm; width 2.6 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.5–4.7 mm long and 2.5–2.6 mm wide. Additionally, specimens vary slightly in color and luster from dark brown to black, and from slightly metallic to not metallic. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species, *L. leeanneae*, is named in honor of intrepid conservation biologist Dr. Leeanne Alonso, who led the expedition to Suriname on which this beetle was collected, as well as many others that have documented the biodiversity of the Guiana Shield.

Habitat and Distribution. This species is only known from the type locality at Kasikasima, Sipaliwini District, Suriname (Fig. 38). All specimens were collected in a UV light trap, so the exact microhabitat is unknown. The light was situated in a densely forested area less than 25 meters from the Palumeu River. Numerous other small creeks and forest pools were within 500 meters of the site. However, the biology is likely to be similar to other species from the region – they inhabit leaf packs and waterlogged woody debris in streams and rivers.

***Lutrochus maldonadoi* Maier & Short, 2013**

(Figs. 286–296)

Type Material. Holotype male: "Venezuela Exp.;Culebra N. Duida; Territ. Amazonas; April 7-16 1950" "J. Maldonado; Capriles Coll." "USNM00768075" Holotype deposited in MIZA. (Figs. 292 & 293) **Paratypes (12): VENEZUELA: Amazonas State:** Same locality data as holotype (3 specimens, USNM). "Venezuela Exp.;Territ. Amazonas; Upper Cunucunuma; Julian

Apr. 28, 1950" "J. Maldonado; Capriles Coll." (8 specimens, USNM). Paratypes deposited in: 1 in MIZA, 1 in MALUZ, 2 in SEMC, and 8 in USNM.

Diagnosis. This species can be distinguished from all other described Lutrochidae by the following combination of characters: apical metatarsomere entirely pubescent, apical maxillary palpomere broadly ovate, and metatibia entirely pubescent. It most closely resembles *Lutrochus gimmeli* **n. sp.** from Ecuador.

Redescription. HOLOTYPE MALE. – Length 3.1 mm; width 1.6 mm. Body ovate to parallel-sided and strongly convex, dark to medium brown, densely pubescent; clothed with short, fine, recumbent setae and long, erect golden setae (Fig. 286).

Head broad, broadly rounded, strongly grooved beneath eye for reception of antenna (Fig. 289). Eye rounded, large, with short, golden interfacetal setae; eyes slightly projecting from outline of head. Antenna short, reaching slightly past anterior border of pronotum, apical 9 antennomeres short, dark brown and clavate, clothed with short golden setae (Fig. 289). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae longer laterally, nearly as long as labrum. Apical margin of labrum sinuate, apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with sparse setae. Mandibles large, dark brown, falciform; apex of mandible with one or two blunt teeth, if with two teeth, weakly so. Maxilla with 4-segmented palpus, apical palpomere flattened and ovate. Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, two times as wide as long at base, bisinuate at base. Lateral edge of pronotum with distinct bead, slightly explanate apically (Fig. 288). Posterior margin straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, slightly wider than

long; clothed in golden setae, which rest transversely, appearing silver to whitish in dorsal view. Hypomeron slightly excavate posteriorly to accommodate profemur (Fig. 288).

Elytron pubescent, dark brown to medium brown, widest at anterior third. Elytron broadly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; elytron clothed with dense short recumbent golden setae and long erect golden setae; humerus not protuberant (Fig. 286). Lateral edge with distinct bead, epipleuron appearing narrow in ventral aspect (Fig. 288). Elytron with faint sutural stria in apical third. Elytral apex broadly rounded.

Prosternum transverse, approximately 1.7 times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, pointed posteriorly (Fig. 287). Mesoventrite pubescent, disc fully clothed with setae. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly to metacoxae.

Legs long and slender, posterior two pairs reddish-brown, anterior pair dark brown. Profemur densely pubescent. Protibia entirely pubescent (Fig. 295). Protarsus with all tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere 1.2 times as long as preceding four tarsomeres combined. Mesocoxa with row of short golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia completely glabrous, with small patch of short golden setae at apex; apex with excavation laterally for reception of tarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.5 times as long as preceding four tarsomeres combined. Metatrochanter globose, slightly pointed posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, with small patch of

longer golden setae at apex (Fig. 295). Metatarsus pubescent, setae becoming sparse toward apex of apical tarsomere, with apical tarsomere as long as previous four combined (Fig. 296).

Abdomen densely pubescent, with five ventrites. First abdominal ventrite shallowly excavated for reception of folded hind legs (Figs. 291 & 287). Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres1.4 mm long. Aedeagus slender and curved, becoming more curved at tapered tip (Fig. 294). Parameres fused, pointed, with distinct lobes interiorly subapically.

Female. Length 2.8 mm; width 1.4 mm. Externally similar to male.

Intraspecific Variation. This species varies considerably in size, ranging from 2.5–3.2 mm long and 1.4–1.6 mm wide. Additionally, specimens vary slightly in color, from dark brown to medium brown. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease, or the grease changes the apparent color of the setae to brown.

Habitat and Distribution. This species was collected at the same collecting events as *L. gustafsoni,* in Amazonas State, Venezuela (Fig. 39). The habits and microhabitat preferences of this species are unknown.

Lutrochus misellus Grouvelle, 1896

Type description from Grouvelle 1896. Translation from original description in French. "*Lutrochus misellus* n. sp. -very similar to *L. germari* , but smaller and with longer vetsiture - length 4 mill. Very similar *L. germari*, Grouv., But much smaller and covered with a fairly thick and hairy enough longer. Reddish legs. Brazil. (Nova Friburgo). Collection R. Oberthur." Also,

the key indicates that this species has "*Tranche externe des tibias intermidiares comprimée, silonnee à l'extremite, présentant á la base de ce sillon un petit sinus formant un angle obtus* [Outer-middle shins compressed, furrowed in extremity, presenting at the base of this groove a small sinus forming an obtuse angle]" – indicating that it possesses the apical excavation of the mesotibia This character defines the genus *Lutrochus* (other than the West Indian species *Berotrochus geniculatus*) and supports the placement of this species in that genus.

Habitat and Distribution. This species is known only from a single specimen for the type locality, Nova Friburgo, Rio de Janiero, Brazil. Nova Friburg is a mountainous area located in dense tropical forest in the Atlantic Forest region of Brazil (Fig. 40).

Remarks. A thorough search of the MNHN by several individuals (A.E.Z. Short, A. Mantilleri, & S. Baca) on two occasions, did not recover the type of this species, therefore it was not examined for the current study. No specimens identified as this species are known, and the vague nature of the description makes it very difficult to match undetermined specimens to this species name.

As part of the current study, we exampined a single adult specimen of *Lutrochus* from Campos de Jordão, São Paolo Brazil that does not match *Lutrochus germari* (the type locality of that species is in Teresopolis, Brazil, just 50 km to the South of the type locality of *L. misellus*). This specimen may belong to *L. misellus.* We hesitate to assign a name to this specimen, though, in a case when the species identity is so ambiguous.

Other Material Examined (not assigned to *L. misellus*). BRAZIL: Rio de Janiero: "Campos de Jordão, SP; Parque Estadual; 1987.; Oliviera, L.G. &; C.G. Froehlich; Lutrochus germairi; No 2689"

***Lutrochus montanus* Grouvelle, 1896**

(Figs. 297–303)

Type Material. Lectotype male (here designated): "Yungas de; Cochabamba; Bolivia" "MUSEUM PARIS; 1917; Coll. Grouvelle" "CReAC003115" "LECTOTYPE; Lutrochus montanus, Grouvelle, 1896, des. Maier & Short 2015." Lectotype deposited in MNHN. (Figs. 301 & 302) **Paralectotypes (15). BOLIVIA: La Paz**: Same locality data as lectotype. (14 specimens, MNHN, 1 specimen, BMNH).

Other Material Examined: See Appendix V for complete list.

Diagnosis. This species is most similar to others in the *Lutrochus montanus* species group. These are united by the completely bare hind tarsi and rectangular shape of the apex of the parameres in lateral aspect (Fig. 300). *Lutrochus montanus* can be separated from *L. violaceus* by the completely densely pubescent apical protarsomere when viewed from above (Fig. 303), and from *L. barrae* by the apex of the parameres not extended posteriorly when viewed laterally (Fig. 300). Additionally, the elytral humeri in *L. montanus* are nearly smooth within the outline of the body, as opposed to protuberant in *L. barrae* and *L. violaceus*.

Redescription. LECTOTYPE MALE. – Length 4.6 mm; width 3.1 mm. Body slightly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, recumbent, dark bronze setae (Fig. 297).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna short, reaching slightly past anterior border of pronotum; antennomeres brunneous; antennomeres short and clavate, nearly serrate, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with dense

golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.75 times as wide as long at base, bisinuate at base (Fig. 297). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 299). Posterior margin gentl curved anterior to scutellum. Disc broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 299).

Elytron pubescent, clothed with dense, short, recumbent dark bronze setae, medium brown, widest at anterior third. Elytron strongly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not protuberant, within outline of body (Fig. 297). Lateral edge with distinct and weakly sinuate bead (Fig. 299). Elytron lacking faint sutural stria in apical third. Elytral apex rounded.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, rounded posteriorly (Fig. 298). Disc with weak carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, dark brown. Procoxae transverse. Profemur densely pubescent, dark brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, lacking dense patch of long golden setae apically (Fig. 303), excavate dorsally to receive protarsus,

explanate laterally (Fig. 298). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, glabrous ventrally, densely pubescent nearly to apex dorsally (Fig. 303). Mesocoxa with tuft of short golden setae basally. Mesofemur with gently arching margins; densely pubescent posteriorly, becoming less so anteriorly, dark brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with one distinct longitudinal carina (Fig. 299); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with two weak posterior projections. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae; apex glabrous, lacking fringe of setae. Metatarsus with all tarsomeres entirely glabrous, as in Fig 303, apical tarsomere as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 298). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation reaching nearly to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 2.0 mm long. Aedeagus slender and strongly curved at apex. Parameres fused, pointed, apex of fused parameres squarish in shape, apex nearly rectanglular, lobes not extended at apex (Fig. 300).

Female. Length 5.7 mm; width 2.7 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.5–5.7 mm long and 2.7–3.6 mm wide. Additionally, specimens vary slightly in color and luster from dark

brown to black, and from slightly metallic to not metallic. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. This species is known from throughout the Southern Andes Mountains, from southern Peru to Bolivia (Fig. 41). It appears to prefer high altitude streams, much like other species in the group, with all known specimens collected over 3,000 m.

Remarks. This type series of this species is made up of a series of syntypes, designated as such by the describer, Grouvelle. This series was surprisingly difficult to find, but was located by Stephen Baca (University of Kansas) in the Grouvelle collection at the MNHN. These specimens match the type locality in the original publication (Yungas de Cochabamba, Bolivia), but do not bear "Type" labels. The identification labels match Grouvelle's handwriting, so this series, while it lacks "Type" labels, is assumed to be the type series. Here, we designate a single male specimen as lectotype, which has had its genitalia dissected and illustrated. We have removed it from the card and it now bears lectotype labels. All other specimens in the series are now designated as Paralectotypes. Additional evidence for this series being the type series is a single specimen with the same style of label, from the same locality, deposited in the BMNH, which bears a round, yellow "Co-type" label.

***Lutrochus pilula* Erichson, 1847**

(Figs. 304–311)

Type Material. *Lutrochus pilula:* two syntypes in ZMHB. **Lectotype female (here designated)**: [pinned] "Hist.-Coll. (Coleoptera); Nr. 9569; Lutrochus pillulua [*sic*] Germ. i.; litt.; Brasil., Germ.; Zool. Mus. Berlin [green label, typed]" "SYNTYPUS; Lutochrus [*sic*] pilula; Erichson, 1847; labelled by MNHUB 2011 [red label, printed]" "LECTOTYPE; *Lutrochus pilula*;

Erichson, 1847; des. C. A. Maier 2015 [yellow label, printed]" "CReAC003059; Aquatic Beetle Database". (Figs. 309 & 310). **Paralectotype female (one paralectotype, here designated)**: [pinned] "pillula; Germ. i. litt.; Brasil. Germ. [blue label, handwritten]" "9569 [weathered white paper, typeset]" "Hist.-Coll. (Coleoptera); Nr. 9569; Lutrochus pillulua [*sic*] Germ. i.; litt.; Brasil., Germ.; Zool. Mus. Berlin [green label, typed]" "SYNTYPUS; Lutochrus [*sic*] pilula; Erichson, 1847; labelled by MNHUB 2011 [red label, printed]" "PARALECTOTYPE; *Lutrochus pilula*; Erichson, 1847; des. C. A. Maier 2015 [light blue label, printed]" "CReAC003058; Aquatic Beetle Database".

Other Material Examined: ARGENTINA: Entre Rios: "ARGENTINA:E.R.; Salto Grande; Rio Uruguay; 16 Nov 1973; O.S. Flint Jr." "USNM ENT; 717782" (Possibly a male of *L. pilula*? Genitalia as illustrated (Fig. 307))

Diagnosis. *Lutrochus pilula* is most similar to *L. germari* in body form, size, and pattern of setation of the tibiae and tarsi these two species are overlap in geographic range (Both are from Brazil). It can be distinguished from this species by its very short antennae and the setation pattern of the protarsi. In *L. pilula*, the apical protarsomere is glabrous in the apical two thirds, while in *L. germari*, the apical protarsomere is tomentose in the apical two thirds.

Redescription. LECTOTYPE FEMALE. – Length 4.5 mm; width 2.5 mm. Body broadly ovate and strongly convex, dark brown to black, densely pubescent; clothed with very short, fine, recumbent, golden setae (Fig. 304).

Head broad, broadly rounded, strongly grooved beneath eye for reception of antenna, nearly carinate. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head (Fig. 304). Antenna very short, barely reaching anterior border of pronotum; antennomeres brunneous; antennomeres III–XI forming a dense club (Fig. 308). Frontoclypeal

suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, lacking golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere somewhat flattened.

Pronotum pubescent, dark brown, 2.0 times as wide as long at base, bisinuate at base (Fig. 304). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 306). Posterior margin not emarginate anterior to scutellum (Fig. 304). Disc broadly convex. Scutellum nearly twice as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 306).

Elytron pubescent, clothed with dense, very short, recumbent dark bronze setae, dark brown, widest at anterior third; setae not arranged in rows. Elytron strongly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not protuberant (Fig. 304). Lateral edge with distinct and weakly sinuate bead (Fig. 306). Elytron without sutural stria. Elytral apex broadly rounded.

Prosternum transverse, a little less than two times as wide as long; anterior edge with strong bead, not deflexed to accommodate withdrawn head; prosternal process wider than long, with bead laterally, rounded posteriorly (Fig. 305). Disc with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, dark brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent,

lacking dense patch of long golden setae apically (Fig. 304), only slightly expanded and excavate dorsally to receive protarsus, only slightly explanate laterally (Fig. 305). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere about as long as preceding four tarsomeres combined, glabrous in apical two thirds, tomentose in basal one third (Fig. 311). Mesocoxa with tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, medium brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin expanded, with one distinct longitudinal carina (Fig. 305); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa with lacking distinct posterior projections. Metatrochanter globose, carinate posteriorly, not excavate, lacking posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere glabrous, as in Fig. 311, 1.25 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 305). First abdominal ventrite distinctly sinuate, shallowly excavate for reception of folded hind legs, excavation reaching two thirds of way to posterior edge of ventrite. Apical ventrite obtusely pointed.

Male. Male of this species is unknown, though a single specimen from Salto Grande, Argentina possesses the same short antennae of the types of *L. pilula*, and may belong to this species. The genitalia of this specimen are as illustrated (Fig. 307).

Intraspecific Variation. This species varies slightly in size, ranging from 4.5–4.7 mm long and 2.5–2.6 mm wide. Additionally, specimens vary slightly in color and luster from dark

brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. This species is known only from the type locality, which, unfortunately, was only noted as "Brasil" on labels and in Erichson's original publication. A third specimen, from Salto Grande, in northeastern Argentina, may also belong to this species. It is also interesting to note that the Argentina *L. pilula* specimen was collected from Salto Grande in 1973, one year before a large hydroelectric dam was constructed on the Uruguay River, possibly destroying the habitat. Based on this specimen's affinities to *L. pilula*, we hypothesize that *L. pilula* is likely from far southern Brazil (Fig. 42).

Remarks. *Lutrochus pilula* is a rather rare species, as examination of nearly 400 specimens of *Lutrochus* from Brazil didn't turn up any additional specimens besides the types. The distinctive antennae separate this species from the widespread species, *Lutrochus germari*.

***Lutrochus tocache* n. sp.**

(Figs. 312–319)

Type Material. Holotype: "ECUADOR: Napo; Cuyabeno (20 km W); on Aguarico; 24 April 1976; J. Cohen BlkLite" "USNM ENT; 00717925" Holotype deposited in USNM. (Figs. 317 & 318) **Paratypes (77). ECUADOR: Napo:** Same locality data as Holotype (75 specimens, USNM). "ECUADOR E; Napo River, 340 m; 70 km E Puerto Napo; 27 I 2011 M. Snižk" (2 specimens, WDSC). **Pastaza:** "ECUADOR: Pastaza; confluence Rio Macuma; & Rio Morona, 300 m; VII:17:1971 B. Malkin" (3 specimens, FMNH). **PERU: Amazonas:** "Peru, S.A.; Aug 14 1936; F. Woytkowski; No. 3756" "Guayabamba subt. Val.; 70 km E. of Chachapoya; Dept. Amazonas" (1 specimen, SEMC). **Huanuco:** "PERU: Huanuco; Tingo Maria 670 m.; 1-10 May

1937; F. Woytkowski" (2 specimens, SEMC). "PERU: Huanuco; Tingo Maria region; 25 June-5 July 1937; F. Woytkowski" (4 specimens, SEMC). "PERU: Huanuco; Tingo Maria region; 15–24 June 1937; F. Woytkowski" (6 specimens, SEMC, 5 specimens, OMNH). "Peru, S.A.; Dec. 11–30 1937; F. Woytkowski; No. 3811" "Department Huanuco; Vic. Leonpampa; Jungle 800 m.a.s.l." "H.E. Hinton; collection; B.M. 1977-566" (5 specimens, BMNH). **San Martin:** Peru, S.A.; Oct. 18 1933; F. Woytkowski; No. 3758" "Soritor; 21 km W of Rioja; Dept. San Martin" (1 specimen, SEMC). "PEROU; PROV. HUALLAGA; TOCACHE 500; G.A. BAER 10.11.1900" "MUSEUM PARIS; 1917; Coll. Grouvelle" (3 specimens, MNHN).

Diagnosis. *Lutrochus tocache* is most similar to *L. vestitus* in the pattern of setation of the tibiae and tarsi. It can be distinguished from this species by its larger size, elongate, parallel-sided body form, the distinctive pattern of pilosity on the elytra, which is arranged in subtle longitudinal rows. The pro- and mesotibiae of *L. tocache* are also expanded laterally, instead of simply flattened, as in *L. vestitus*.

Description. HOLOTYPE MALE. – Length 5.2 mm; width 3.0 mm. Body elongate-ovate and weakly convex, dark brown to black, densely pubescent; clothed with short, fine, recumbent, dark bronze setae (Fig. 312).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna long, reaching well past anterior border of pronotum; antennomeres brunneous; antennomeres long and slightly serrate, nearly filiform, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of

mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.0 times as wide as long at base, bisinuate at base (Fig. 312). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 314). Posterior margin slightly emarginate anterior to scutellum (Fig. 312). Disc broadly convex. Scutellum slightly diamond-shaped, about as wide as long; clothed in recumbent slivery setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 314).

Elytron pubescent, clothed with dense, short, recumbent dark bronze setae, medium brown, widest at anterior third; setae arranged in faint rows, with distinct, very narrow, longitudinal glabrous patches. Elytron weakly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not protuberant (Fig. 312). Lateral edge with distinct and weakly sinuate bead (Fig. 314). Elytron with faint sutural stria in along entire length. Elytral apex slightly acuminate.

Prosternum transverse, a little less than two times as wide as long; anterior edge with weak bead, not deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acute posteriorly (Fig. 313). Disc smooth, lacking carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, dark brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, with dense patch of long golden setae apically (Fig. 312), strongly expanded and excavate dorsally to receive protarsus, explanate laterally (Fig. 312). Protarsus with basal four tarsomeres densely

pubescent, lacking tufts of long golden setae ventrally; apical tarsomere 1.25 times as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 319). Mesocoxa with tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, medium brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin greatly expanded, with two distinct longitudinal carinae (Fig. 314); apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.25 times as long as preceding four tarsomeres combined. Metacoxa with two very weak posterior projections. Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only at base, as in Fig 319, 1.25 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 313). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation only reaching halfway to posterior edge of ventrite. Apical ventrite obtusely pointed.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus slender and curved. Parameres fused, pointed, lobes slightly extended at apex (Fig. 315).

Female. Length 5.7 mm; width 3.3 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.7–5.7 mm long and 2.4–3.3 mm wide. Additionally, specimens vary slightly in color and luster from dark

brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species was first noted as a distinct by Grouvelle, as *Lutrochus* "baeri," an MS name (MNHN). However, the name "baeri" was very similar to "barri" and had the potential to cause confusion with the aforementioned species, so the name *Lutrochus tocache* was chosen, in reference to the locality where the species was first collected, in 1900 in Tocache, Peru.

Habitat and Distribution. This species has been recorded from the eastern foothills of the Andes Mountains, restriced to tributaries to the Napo River, in the Amazon River drainage, ranging from Eastern Ecuador to Northern Peru (Fig. 43).

Remarks. *Lutrochus tocache* has a unique body shape among species of *Lutrochus*, with a shallowly convex body, which is narrowly ovate in dorsal aspect. The sides of the body are remarkably parallel, a body shape shared only with *Lutrochus torrens* **n. sp**.

Lutrochus torrens **Maier & Short n. sp.**

(Figs. 320–328)

Type Material. HOLOTYPE MALE: "COSTA RICA: San José; Prov., trib. Rio Pacuar; at Hwy. 2 15 rd. Km N of; San Isidro de General; 21-VI-2001" "09˚26'16" N; 83˚40'41" W; elevation 4880 ft; just N Horquetas" "HOLOTYPE; Lutrochus torrens; des. Maier & Short 2015" Holotype deposited in EMEC. (Figs. 324 & 325) **Paratypes (9). COSTA RICA: San José:** Same locality data as Holotype (4 specimens, EMEC). **Cartago:** "Cartago Province; Tapanti Nat. Park 18–19.ii.2010; 09˚45.540'N, 83˚ 47.596' W; 1345 m; Trail at Kiri Lodge; leg. Short et al.; FIT; CR10-0317-TN1.1" (1 specimen, SEMC). "Cartago Province; Tapanti Nat. Park 18-

19.ii.2010; 09˚45.540'N, 83˚ 47.596' W; 1345 m; Trail at Kiri Lodge; leg. Short et al.; FIT; CR10-0317-TN1.1" (1 specimen, SEMC). CR11-0716-02B (3 specimens, SEMC). "COSTA RICA: Cartago; Prov. sm. Stream 5.1 rd km; SE of park entrance; 22-VI-2003, C.B. Barr" (1 specimen, EMEC).

Diagnosis. *Lutrochus torrens* **n. sp.** is most similar to *L. tocache* **n. sp.** in body shape and the pattern of setation of the tibiae and tarsi. It can be distinguished from this species by the presence of patches of elongate golden setae at apex of pro- and metatibiae (these are absent in *L. tocache* **n. sp.**), and the lack of patterns in the elytral setae (Fig. 320). The protibiae of *L. torrens* **n. sp.** are also somewhat cylindrical (Fig. 321), as opposed to expanded, as in *L. tocache* **n. sp** (Fig. 313).

Description. HOLOTYPE MALE. – Length 4.9 mm; width 2.9 mm. Body ovate and weakly convex, reddish-brown to dark brown, densely pubescent; clothed with very short, fine, erect, golden setae (Fig. 320).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna long, reaching well past anterior border of pronotum; basal antennomeres rufous, apical antennomeres brunneous; antennomeres long and slightly serrate, nearly filiform, clothed with short golden setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae 1.5x as long as medial setae. Labrum clothed with sparse and short golden setae. Mandibles large, dark brown, falciform; apex of mandible with 2 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, 2.0 times as wide as long at base, bisinuate at base (Fig. 320). Lateral edge of pronotum with distinct bead, borders not explanate (Fig. 322). Posterior margin straight anterior to scutellum (Fig. 320). Disc broadly convex. Scutellum triangular, about as wide as long; clothed in short, erect, golden setae. Hypomeron excavate posteriorly to accommodate profemur (Fig. 322).

Elytron pubescent, clothed with dense, very short, erect golden setae, medium brown, widest at halfway down length; setae randomly distributed, with lacking any longitudinal glabrous patches. Elytron weakly convex, densely punctate, with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; humerus not protuberant (Fig. 320). Lateral edge with distinct and weakly sinuate bead (Fig. 322). Elytron lacking sutural stria. Elytral apex rounded.

Prosternum transverse, 1.5 times as wide as long; anterior edge with weak bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, strongly acute posteriorly (Fig. 321). Disc smooth, with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae, with distinct marginal carinae laterally; transverse sulcus nearly straight. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron not explanate, narrowing posteriorly to metacoxae.

Legs long and slender, reddish brown. Procoxae transverse. Profemur densely pubescent, medium brown, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, with dense patch of long golden setae apically (Fig. 321), not expanded, cylindrical, excavate dorsally to receive protarsus, not explanate laterally (Fig. 320). Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere 1.5 times as

long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally, pubescence thinning toward apex (Fig. 328). Mesocoxa with tuft of short golden setae basally. Mesofemur with nearly parallel sides; densely pubescent, reddish brown. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin barely expanded, with distinct longitudinal carina (Fig. 322); apex with excavation laterally for reception of mesotarsus, excavation reaching nearly one third way up length of tibia. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere 1.5 times as long as preceding four tarsomeres combined. Metacoxa with one very weak posterior projection. Metatrochanter globose, excavate posteriorly, with strong posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band dorsally; with short, golden setae, lacking fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only at base, as in Fig. 319, 1.5 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 321). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation only reaching halfway to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 2.4 mm long. Aedeagus slender and curved. Parameres fused, pointed, lobes slightly extended at apex (Fig. 323).

Female. Length 5.5 mm; width 3.1 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies slightly in size, ranging from 4.7–5.5 mm long and 2.7–3.1 mm wide. Additionally, specimens vary slightly in color and luster from dark

brown to black. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named "torrens" from the Latin word for a stream or torrent, referring to the fast moving waterfall habitats where many specimens of this species were found.

Habitat and Distribution. This species has been recorded from the central mountains of Costa Rica, in the Rio Orosí drainage, and in the region surrounding Tapantí National Park (Fig. 44). All specimens were collected at high elevation (above 1200 m).

This species prefers submerged dead wood in fast moving, cool mountain streams, and one series was collected at the base of a ~40 foot waterfall in Tapantí National Park, Costa Rica (Fig. 327).

***Lutrochus vestitus* (Sharp, 1882)**

(Figs 329–338)

Byrrhomorphus vestitus Sharp, 1882

Type Material. Holotype Female: "Byrrhomorphus vestitus; D.S.; Type; Panima Vera Paz.; Guatemala; Champion [on card-mounted specimen" "Panima, Guatemala, Champion" "Type [Round label; red border]" "Sharp Coll." "B.C.A. Col. I.2.; Byrrhomorphus vestitus; Sharp" "♀" "CreAC003107" Holotype deposited in BMNH. (Figs. 335–338)

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species is hardly distinctive externally, and shares a great number of characters with some closely related species. The pattern of setation on the legs, while usually a good character for distinguishing species, provides no information with this species. Lutrochus vestitus shares its setation pattern (see Fig. 334) with four other species of *Lutrochus* - *L. wao*, *L.*

funkae, *L. germari*, and *L. guarani*. It can be distinguished from the preceeding species based on the morphology of the male genitalia.

Redescription. MALE. – Length 3.6 mm; width 2.1 mm. Body wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, slightly recumbent golden setae and long, erect golden setae (Fig. 329).

Head broad, broadly rounded. Eye rounded, large, with short, golden interfacetal setae; eyes slightly projecting from outline of head. Antenna long, reaching past anterior border of pronotum, apical 9 antennomeres dark brown and clavate, clothed with short golden setae, proximal antennomeres testaceous (Fig. 330). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae half as long as labrum. Apical margin of labrum sinuate, with short apical setal brush. Labrum clothed with sparse, golden setae. Mandibles large, dark brown, falciform; apex of mandible with three blunt teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex (Fig. 331). Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, 2.5 times as wide as long at base, bisinuate at base. Lateral edge of pronotum with distinct bead, broadly rounded (Fig. 329). Posterior margin straight anterior to scutellum. Disc of pronotum broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, dark brown to medium brown, widest at anterior fourth. Elytron broadly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; elytron clothed with dense, short, recumbent golden setae and long, erect, golden setae; humerus slightly protuberant (Fig. 329). Lateral edge with distinct

bead, appearing narrow in ventral aspect (Fig. 330). Elytron with very weak sutural stria in apical fourth. Elytral apex slightly acuminate.

Prosternum transverse, approximately 1.6 times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process slightly wider than long, without bead laterally, obtusely angled posteriorly (Fig. 330). Mesoventrite pubescent, disc fully clothed with setae. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 330). Mesepimeron extended posteriorly to metacoxae.

Legs long and slender, dark brown to black. Profemur densely pubescent. Protibia entirely pubescent . Protarsus with proximal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere as long as preceding four tarsomeres combined, pubescent dorsally and glabrous ventrally. Mesocoxa with tuft of short golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia glabrous, with many scattered setae; apex with excavation laterally for reception of tarsus and notch proximal to excavation (Fig. 334). Mesotarsus entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metatrochanter globose, with pointed projection posteriorly. Metafemur densely pubescent. Metatibia pubescent to apical sixteenth, apical sixteenth glabrous. Metatarsus with proximal four tarsomeres entirely pubescent; apical tarsomere glabrous, as long as previous four combined (Fig. 334).

Abdomen densely pubescent, with five ventrites (Fig. 330). First abdominal ventrite shallowly excavated for reception of folded hind legs. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.8 mm long. Aedeagus slender and evenly curved, with slight notch at tapered tip (Fig. 332). Parameres fused, pointed, with distinct lobes interiorly subapically.

Female. Length 4.2 mm; width 2.1 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 3.0–4.5 mm long and 1.6–2.2 mm wide. Additionally, specimens vary slightly in color and luster – from dark brown to black, and from slightly metallic to not metallic. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Habitat and Distribution. This species is known from small, wooded streams and rivers throughout Central America (45).

The type locality is Panima, Baja Verapaz Department, Guatemala. Interestingly, while the exact locality is not known, several carbonate, or karst, rivers flow through this region in the Sierra de las Minas range. Lutrochus vestitus may prefer streams flowing through karst regions, as species in *Auritrochus* do.

Remarks. Species which were morphologically similar to *Lutrochus vestitus* have been identified in the past as this species. However, a phylogenetic study has since revealed that Lutrochus vestitus in its current state is polyphyletic.

We suggest that *L. vestitus* is actually a species complex, made up of several cryptic species, and the species requires further study.

***Lutrochus violaceus* Maier & Short, 2013**

(Figs. 339–360)

Type Material. Holotype male: "VENEZUELA:Merida State;8° 35.355′ N, 71° 13.926′ W, 1646 m; N. of Ejido, Rt. 4 river x-ing;10.vii.2009; leg. Shepard; gross sample; VZ09-0720-

02Z" "SEMC0929353;KUNHM-ENT". Holotype deposited in MIZA. **Paratypes (66): VENEZUELA: Mérida State:** "VENEZUELA:Merida State; 8° 51.933′ N, 70° 37.131′ W, 1682 m; Cascada Velo de la Novia; 24.i.2012;leg. Short, Arias, & Gustafson; Logs & Kicknetting" (15 specimens SEMC). "VENEZUELA:Merida State; 8° 52.423′ N, 70° 37.611′ W, 1616 m; ca. 12 km SE Santo Domingo;leg. Short, Arias, & Gustafson; 22.i.2012; log and stick jams in; river; VZ12-0122-03B" (44 specimens SEMC). "VENEZUELA:Merida State; 8° 51.933′ N, 71° 37.131′ W, 1682 m; ca. 12 km SE of Santo Domingo;19.vii2009; leg. W. Shepard;gross sample; VZ09-0719-02Z" (5 specimens SEMC). "VENEZUELA:Merida ;Merida at zoo; 14 I 06;Rio Milla; [reverse] AS-06-026" "A.E.Z. Short; P.J. Torres" (2 specimens SEMC). Paratypes deposited in: 1 in MIZA, 1 in MALUZ, 1 in NMW, 61 in SEMC, and 2 in USNM.

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species can be distinguished from all other described Lutrochidae by the distinctive violet sheen dorsally. This species most closely resembles *Lutrochus cauraensis*, and can be separated from that species by the pubescence of the protarsomere. In *L. violaceus*, the apical protarsomere is pubescent, although more sparse in apical half (Figs. 346 & 356), while in *L. cauraensis*, the pubescent area on the apical protarsomere is discrete (Fig. 211).

Redescription. HOLOTYPE MALE. – Length 4.5 mm; width 2.7 mm. Body wedge-shaped and strongly convex, reddish-brown to black, densely pubescent; clothed with short, fine, slightly recumbent and erect golden setae (Fig. 339).

Head broad, broadly rounded. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head. Antenna short, reaching slightly past anterior border of pronotum, medium brown and clavate, clothed with short golden setae (Fig. 354). Frontoclypeal

suture indistinct. Clypeal margin straight, with brush of long black setae apically, setae nearly as long as labrum. Apical margin of labrum sinuate, with apical setal brush, lateral setae three times as long as medial setae (Fig. 351). Labrum clothed with sparse golden setae. Mandibles large, dark brown, falciform; apex of mandible with three teeth (Fig. 352). Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex (Fig. 353). Labial palpus 3-segmented; apical palpomere fusiform (Fig. 355).

Pronotum pubescent, 2.2 times as wide as long at base, bisinuate at base (Fig. 339). Lateral edge of pronotum with distinct bead, broadly rounded. Posterior margin slightly notched anterior to scutellum. Disc of pronotum broadly convex. Scutellum sub-triangular, about as wide as long (Fig. 345). Hypomeron excavate posteriorly to accommodate femur.

Elytron pubescent, dark brown, with slight bluish to violet metallic sheen, widest at basal one third. Elytron broadly convex, densely punctate with very fine, shallow punctures, punctures randomly scattered, not arranged in rows; elytron clothed with dense, short, recumbent golden setae and short, erect, golden setae; humerus not protuberant (Fig. 339). Lateral edge with distinct bead (Fig. 341); elytral epipleuron appearing narrow in ventral aspect (Fig. 340). Elytron with very weak sutural stria in apical fourth (Fig. 339). Elytral apex slightly acuminate.

Prosternum transverse, approximately 1.6 times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, lacking lateral bead, broadly rounded posteriorly (Fig. 340). Disc of mesoventrite entirely pubescent. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs (Fig. 348). Mesepimeron extended posteriorly to metacoxae.

Legs long and slender, reddish-brown. Profemur densely pubescent. Protibia entirely pubescent . Protarsus with basal four tarsomeres pubescent, with tufts of golden setae ventrally;

apical tarsomere 1.2 times as long as preceding four tarsomeres combined, glabrous ventrally, pubescent dorsally (Fig. 346). Mesocoxa with tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia completely glabrous, with small patch of golden setae at apex; apex excavated for reception of tarsus (Fig. 349). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere 1.2 times as long as preceding four tarsomeres combined. Metatrochanter globose, with small posterior projection. Metafemur densely pubescent. Metatibia entirely pubescent, except apical 1/16 glabrous. Metatarsus entirely glabrous, with apical tarsomere as long as previous four combined (Fig. 343).

Abdomen densely pubescent, with five ventrites (Fig. 347). First ventrite shallowly excavated for reception of folded hind legs. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 2.6 mm long. Aedeagus slender and straight, becoming slightly curved just before tapered tip. Parameres fused, pointed, with distinct lobes interiorly subapically (Fig. 357).

Female. Length 5.1 mm; width 2.9 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 4.5–5.5 mm long and 2.7–3.0 mm wide. Additionally, specimens vary slightly in color and luster – from dark brown to black, and from slightly metallic to not metallic. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species is named “violaceus” because of the presence of a blue-violet sheen on the elytra, which is unique among described Lutrochidae.

Habitat and Distribution. This species is known from several localities in the Mérida Andes, all of which are at elevations above 1500 m (Fig. 46). Specimens of *L. violaceus* have been found clinging to logs and woody debris in small to medium sized (2–7 m wide) mountain streams (Fig. 360).

***Lutrochus wao* Maier & Short, 2014**

(Figs. 361–368)

Type Material. Holotype male: "GUYANA: Region 9; Parabara, trail on N. side of river; 2° 6' 29.52"N; 59° 13' 39.183"W 274m; 3-xi-2012; Short, Isaacs, Salisbury; small stream; GY13-1103-02A" Holotype deposited in CBDUG (Figs. 365 & 366). **Paratypes (12): GUYANA: Region 9:** Same locality data as holotype. Paratypes deposited in: 1 in BMNH, 10 in SEMC, 1 in USNM.

Other Material Examined: FRENCH GUIANA: "FG: Sinnemary/26 Nov 2007/Queney – Road St. Elye/Sa" (7 specimens SEMC, 2 specimens NMHN, 5 specimens PQC). "FG: Mana/ P. Queney – 15 Feb 04/ Road in forest of Crique/ Daranelles" (2 specimens, SEMC, 2 specimens NMHN, 1 specimen PQC). "FG: Seint Laurent du Maroni/ Balete ouest – crosses farm/ 30.i.2005 P. Queney/ Saint Jean" (3 specimens SEMC, 2 specimens NMHN, 1 specimen PQC). "FG: Sinnamary/ 26.i.2003, P. Queney/ Route Jojo" (6 specimens SEMC, 3 specimens NMHN, 4 specimens PQC).

Diagnosis. This species can be distinguished from all other described Lutrochidae by the following combination of characters: antennomeres I–III testaceous below; epipleuron gradually narrowing posteriorly to metacoxae; apical tarsomeres entirely dark brown; apical metatarsomere

pubescent for at least half of length when viewed dorsally (Fig. 367); parameres of male genitalia with weak crenulations at apical border (Fig. 364).

Redescription. HOLOTYPE MALE. – Length 4.1 mm; width 2.1 mm. Body ovate and convex, dark brown to black, densely pubescent; clothed with short, fine, erect golden setae (Fig. 361).

Head broad, broadly rounded, very weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes slightly bulging from outline of head. Antenna short, reaching slightly past anterior border of pronotum; antennomeres 1–3 testaceous below, brunneous above, antennomeres 4–11 brunneous; antennomeres short and clavate, clothed with short golden setae and longer dark setae. Frontoclypeal suture indistinct. Clypeal margin straight. Apical margin of labrum broadly rounded, with golden apical setal brush, lateral setae twice as long as medial setae. Labrum clothed with long golden setae. Mandibles large, dark brown, falciform; apex of mandible with 3 distinct teeth. Maxilla with 4-segmented palpus, apical palpomere flattened and rounded-triangular; Labial palpus 3-segmented; apical palpomere cylindrical.

Pronotum pubescent, dark brown, reddish-brown near margins, 1.6 times as wide at base as long, bisinuate at base (Fig. 361). Lateral edge of pronotum with distinct bead, only very slightly explanate apically. Posterior margin straight anterior to scutellum. Disc broadly convex. Scutellum triangular, as wide as long; clothed in recumbent golden setae. Hypomeron excavate posteriorly to accommodate profemur.

Elytron pubescent, clothed with dense, short, recumbent golden setae, medium brown, faintly reddish-brown near margins, widest at halfway point, posterior half gently rounded. Elytron shallowly convex, densely punctate with very fine, shallow punctures, punctures

randomly scattered, not arranged in rows; humerus slightly protuberant (Fig. 361). Lateral edge with distinct and weakly sinuate bead (Fig. 363). Elytron lacking faint sutural stria in apical third. Elytral apex rounded, but slightly acuminate.

Prosternum transverse, approximately two times as wide as long; anterior edge with weak bead, deflexed to accommodate withdrawn head; prosternal process about as wide as long, without bead laterally, acute posteriorly (Fig. 362). Disc with carinae to accommodate profemora laterally. Metaventrite pubescent, disc fully clothed with setae. Mesepisternum and epipleuron excavated to accommodate folded front and middle legs. Epipleuron gradually narrowing posteriorly to metacoxae.

Legs long and slender, reddish-brown. Procoxae transverse. Profemur densely pubescent, reddish-brown dorsally, medium brown ventrally, strongly excavate ventrally to receive protibia. Protibia entirely pubescent, excavate dorsally to receive protarsus, only slightly explanate. Protarsus with basal four tarsomeres densely pubescent, lacking tufts of long golden setae ventrally; apical tarsomere entirely dark brown, as long as preceding four tarsomeres combined, glabrous ventrally, pubescent nearly to apex dorsally (Fig. 367). Mesocoxa with tuft of short golden setae basally. Mesofemur fusiform, densely pubescent posteriorly, becoming less so anteriorly, reddish-brown dorsally, medium brown ventrally. Mesotibia completely glabrous, with few scattered setae, lacking small patch of short golden setae at apex; lateral margin not expanded, tibia rounded in cross-section, lacking distinct longitudinal carinae; apex with excavation laterally for reception of mesotarsus. Mesotarsus with all tarsomeres entirely glabrous; apical tarsomere as long as preceding four tarsomeres combined. Metacoxa with single rounded posterior projection. Metatrochanter globose, excavate posteriorly. Metafemur densely pubescent. Metatibia entirely pubescent, except for a narrow, longitudinal glabrous band

dorsally; with short, golden setae, apex with distinct, distally-facing fringe of setae. Metatarsus with basal four tarsomeres entirely pubescent; apical tarsomere pubescent only in basal ½ dorsally and basal one third ventrally as in Fig 367, as 0.9 times as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 362). First abdominal ventrite shallowly excavate for reception of folded hind legs, excavation reaches nearly to posterior edge of ventrite. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.7 mm long. Aedeagus slender and only slighty curved, becoming more curved at base. Parameres fused, pointed, with short distinct lobes interiorly subapically, lobes extended distally at apex (Fig. 367).

Female. Length 4.5 mm; width 2.3 mm. Externally similar to male.

Intraspecific Variation. This species varies slightly in size, ranging from 4.1–4.5 mm long and 2.1–2.3 mm wide. Additionally, specimens vary slightly in color, from dark brown to reddish-brown. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease, or the grease changes the apparent color of the setae to brown.

Etymology. This species is named “wao,” the name for the creek in the local Wapishana language.

Habitat and Distribution. This species is known from Guyana and French Guiana, and is presumably present in Suriname. The type locality is in Region 9, in the southwestern corner of Guyana, near the village of Parabara (Fig. 47). The series was collected in partially submerged leafpacks that were caught behind a fallen branch in a flowing forested stream (Fig. 368). The species is present throughout French Guiana as well, in coastal streams and further inland.

Remarks: This group of species (*Lutrochus vestitus*, *L. wao*, *L. funkae*, and *L. grenadensis*) is fairly well conserved externally, and possesses only subtle internal differences in genitalic morphology, leading to the misidentification of the French Guyana material in Maier & Short (2013) as *L. vestitus*. Based on thorough examination of these specimens, though, we now recognize them as part of a new species, *Lutrochus wao*, distinct from *L. vestitus* of Central America and the Northern Andes.

Most of the species found in the Guianas seem to form a distinct group, along with *Lutrochus vestitus* Sharp. They are united by the unique setation pattern on the protarsus and small size. The one exception is a single Suriname species, *Lutrochus leeanneae*, which bears affinities to *L. cauraensis* Maier & Short and *L. gustafsoni* Maier & Short, both of which are restricted to southern Venezuela.

The sheer number of new species from the region reinforces the idea that this area is poorly collected, and it warrants further collecting effort for Lutrochidae and other aquatic Coleoptera in northern South America.

Saxitrochus Maier & Short

Type Species *Saxitrochus meridaensis* (Maier & Short, 2013)

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Diagnosis. This genus is distinct, and can be distinguished from all other described Lutrochidae by the unique diamond-shaped scutellum (Fig. 374), the glabrous hind tibiae (Fig. 386), the medial circular glabrous patch on the metaventrite (Fig. 380), and the presence of seven shallow rows of punctures on the elytron (369). *Saxitrochus* is also the only known genus in Lutrochidae to inhabit liverwort mats in hygropetric habitats (382).

Redescription. Body length 2.5–3.2 mm and body width 1.4–1.7 mm. Body strongly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with very short, fine, slightly recumbent golden hairs (Fig. 372).

Head broadly rounded, weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head (Fig. 375). Antenna short, reaching slightly past anterior border of pronotum, clothed with short golden setae (Fig. 375). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae nearly as long as labrum. Labrum clothed with sparse, blunt setae, with transverse row of long setae at midline. Mandible large, dark brown, stout, securiform. Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex (Fig. 379. Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, two times as wide as long at base, weakly bisinuate at base (Fig. 369); pronotum lacking basal sublateral carinae. Lateral edge of pronotum with distinct bead, slightly explanate apically (Fig. 371). Posterior margin notched medially to receive pointed anterior margin of scutellum. Disc of pronotum broadly convex. Scutellum diamond-shaped, about as wide as long (Fig. 374). Hypomeron excavate posteriorly to accommodate femur (Fig. 371).

Elytron pubescent, dark brown, with slight metallic sheen, widest at base (Fig. 369). Elytron broadly convex, with seven rows of widely spaced coarse punctures (3 times diameter of punctures); intervals with dense setae; humerus not protuberant (Fig. 369). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 370). Elytral apex slightly acuminate.

Prosternum transverse approximately two times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acuminate posteriorly (Fig. 370). Metaventrite pubescent, with distinct, circular glabrous patch medially (Fig. 376); femoral lines extending nearly to the katepisternal suture, with distinct mesotarsal rests. Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender. Profemur densely pubescent. Protibia mostly pubescent. Protarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres. Mesocoxa with tuft of long golden setae basally. Mesofemur densely pubescent posteriorly, becoming less so anteriorly. Mesotibia curved slightly, completely glabrous, with small patch of golden setae at apex; mesotibia smooth, slightly expanded, apex without excavation laterally for reception of tarsus (Fig. 383). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, with single long seta (twice as long as preceding tarsomere) arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metatrochanter globose, without posterior extensions. Metafemur densely pubescent. Metatibia curved slightly, entirely glabrous, with small patch of golden setae at apex. Metatarsus glabrous, with apical tarsomere as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 370), ventrites constricted medially. Metacoxal rests of first ventrite extending nearly to second ventrite. First ventrite shallowly excavated for reception of folded hind legs. Apical ventrite of male broadly rounded.

Genitalia as illustrated, basal piece + parameres curved and short (relative to *Lutrochus* spp.) ca. 5x as wide as long. Aedeagus slender and very curved, becoming more curved at

tapered tip (Fig. 385). Parameres only slightly fused, pointed, strongly tapering, with distinct lobes interiorly subapically.

Etymology. The generic name *Saxitrochus* is derived from the Latin *Saxi-* for "rock" or "stone", referring to its habitat on rock-face seeps, and *–trochus* in reference to the name of the nominal genus of the family – *Lutrochus*.

Remarks. The species *Saxitrochus meridaensis* is restricted to a single locality (Cascada Velo de la Novia "Bridal Veil Falls", Merida, Venezuela), but its unique habits and morphology, which are unlike any other species of Lutrochidae, warrant its transfer to an entirely new genus.

Comparative Notes. The genus *Saxitrochus* most closely resembles the larger, more robust *Lutrochus*, and it is also distributed in South America like *Lutrochus*. However it possesses several distinct characters which are unique among the Lutrochidae – it is the only genus with both a glabrous mesotibia and glabrous metatibia. It also has a distinct glabrous patch medially on the metasternum and a diamond-shaped scutellum. *Saxitrochus* also lacks the mesotibial excavation, and has the abdominal ventrites constricted medially – characters it shares with the North American *Auritrochus*.

It does have the necessary characters which place it in Lutrochidae – expanded apical maxillary palpomeres (Fig. 379), short, clavate antennae (Fig. 381), and interfacetal setae (Fig. 375) all point clearly to its place in Lutrochidae.

***Saxitrochus meridaensis* (Maier & Short, 2013)**

Lutrochus meridaensis Maier & Short, 2013

(Figs. 369–382)

Type Material. Holotype male: "VENEZUELA:Merida State/8° 52.423′ N, 71° 37.611′ W, 1616 m/ Cascada velo de la Novia/ 19.vii.2009; leg. Short, Gustafson/ Camacho, Garcia, & Inciarte/ VZ09-0719-01A; wet rocks/seeps" "SEMC0881687/KUNHM-ENT". Holotype deposited in MIZA. **Paratypes (13): VENEZUELA: Mérida State:** Same locality data as holotype. Paratypes deposited in: 1 in MIZA, 1 in MALUZ, 1 in NMW, 7 in SEMC (1 on SEM stub), and 3 in USNM.

Other Material Examined. See Appendix V for complete list.

Diagnosis. This species can be distinguished from all other described Lutrochidae by the unique diamond-shaped scutellum, the medial circular glabrous patch on the metaventrite, and the presence of seven shallow rows of punctures on the elytron.

Description. HOLOTYPE MALE. – Length 2.6 mm; width 1.4 mm. Body strongly wedge-shaped and strongly convex, dark brown to black, densely pubescent; clothed with short, fine, slightly recumbent golden hairs (Fig. 372).

Head broad, broadly rounded, weakly grooved beneath eye for reception of antenna. Eye rounded, small, with short, golden interfacetal setae; eyes smooth within outline of head (Fig. 375). Antenna short, reaching slightly past anterior border of pronotum, apical nine antennomeres short, dark brown and clavate, clothed with short golden setae (Fig. 375). Frontoclypeal suture indistinct. Clypeal margin straight, with brush of long setae apically, setae nearly as long as labrum. Apical margin of labrum sinuate, apical setal brush, lateral setae three times as long as medial setae. Labrum clothed with sparse, blunt setae. Mandibles large, dark brown, falciform; apex of mandible with one or two blunt teeth, if with two teeth, weakly so; prostheca with apical field of papilliform sensillae. Maxilla with 4-segmented palpus, apical palpomere flattened and triangular, truncate at apex (Fig. 379); galea with dense apical brush of

setae lateral setae two times as long as medial setae; lacinia shorter and smaller than galea or palpus, with dense brush of curved setae on inner margin. Labial palpus 3-segmented; apical palpomere fusiform.

Pronotum pubescent, two times as wide as long at base, bisinuate at base (Fig. 369). Lateral edge of pronotum with distinct bead, slightly explanate apically (Fig. 371). Posterior margin notched medially to receive pointed anterior margin of scutellum. Disc of pronotum broadly convex. Scutellum diamond-shaped, about as wide as long (Fig. 46). Hypomeron excavate posteriorly to accommodate femur (Fig. 371).

Elytron pubescent, dark brown, with slight metallic sheen, widest at base (Fig. 369). Elytron broadly convex, with seven rows of widely spaced coarse punctures (3 times diameter of punctures); intervals with dense setae; humerus not protuberant (Fig. 369). Lateral edge with distinct bead; epipleuron appearing narrow in ventral aspect (Fig. 370). Elytral apex slightly acuminate.

Prosternum transverse approximately two times as wide as long; anterior edge with strong bead, slightly deflexed to accommodate withdrawn head; prosternal process about as wide as long, with bead laterally, acuminate posteriorly (Fig. 370). Mesoventrite pubescent, with distinct, round glabrous patch medially (Fig. 376). Mesepisternum and mesepimeron excavated to accommodate folded front and middle legs. Mesepimeron extended posteriorly nearly to metacoxae.

Legs long and slender. Profemur densely pubescent. Protibia pubescent to apical ninth. Protarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres; apical tarsomere 1.5 times as long as preceding four tarsomeres combined. Mesocoxa with tuft of long golden setae basally. Mesofemur densely pubescent posteriorly,

becoming less so anteriorly. Mesotibia completely glabrous, with small patch of golden setae at apex; apex without excavation laterally for reception of tarsus (Fig. 383). Mesotarsus with all tarsomeres glabrous, except for tufts of golden setae ventrally on all tarsomeres, with single long seta (twice as long as preceding tarsomere) arising from fourth tarsomere; apical tarsomere as long as preceding four tarsomeres combined. Metatrochanter globose, without posterior extensions. Metafemur densely pubescent. Metatibia entirely glabrous, with small patch of golden setae at apex. Metatarsus glabrous, with apical tarsomere as long as previous four combined.

Abdomen densely pubescent, with five ventrites (Fig. 370). First ventrite shallowly excavated for reception of folded hind legs. Apical ventrite broadly rounded.

Genitalia as illustrated, basal piece + parameres 1.6 mm long. Aedeagus slender and curved, becoming more curved at tapered tip (Fig. 385). Parameres fused, pointed, with distinct lobes interiorly subapically.

Female. Length 3.2 mm; width 1.4 mm. Externally similar to male, females generally larger than males.

Intraspecific Variation. This species varies considerably in size, ranging from 2.5–3.2 mm long and 1.4–1.7 mm wide. Additionally, specimens vary slightly in color and luster – from dark brown to black, and from slightly metallic to not metallic. Some specimens examined have differing levels of setation, with patches where setae have rubbed off, as well as patches where setae have become matted down with grease.

Etymology. This species, *S. meridaensis*, is named for the type locality in Mérida State, Venezuela.

Habitat and Distribution. This species is known only from the type locality, the Cascada Velo de la Novia in Mérida State, Venezuela (Fig. 382). The type series was collected on among liverworts on the seepages and spray zone adjacent to a waterfall (Fig. 382). This is the first known record of the family from hygropetric habitats. A second visit to this locality and other similar nearby habitats during the dry season in 2012 did not yield additional specimens.

This genus, as with most other species in Lutrochidae, may be more widespread than its current distributional map indicates, and warrents further collecting in similar habitats surrounding the Cordillera de Mérida.

KEY TO LUTROCHIDAE ERICHSON SPECIES OF THE WORLD

1 Mesotibia with apical excavation for reception of tarsus (Figs. 182 & 284); West Indies and Central America to South America 2

- Mesotibia lacking apical excavation for reception of tarsus (Fig. 383); North America and Central America and South America along Andes 22

2(1) Body nearly parallel-sided (Fig. 150), mesotibia with small longitudinal patch of setae ventrally (Fig. 152), parameres of male genitalia nearly completely fused to the basal piece (Fig. 153); Greater Antilles **[*BEROTROCHUS*]** ..... ***Berotrochus geniculatus* (Chevrolat)**

- Body ovate, mesotibia completely glabrous, parameres of male genitalia not fused to basal piece; West Indies (Lesser Antilles) and Central America to South America **[*LUTROCHUS*]** ... 3

3(2) Elytra explanate, epipleuron appearing broad in ventral aspect (Fig. 171); reddish-brown in color; prosternum strongly deflexed ventrally in anterior half (Fig. 175); apical maxillary palpomere strongly triangular (Fig. 174) ..... ***Lutrochus acuminatus* Grouvelle**

- Elytra not explanate, epipleuron appearing narrow in ventral aspect (Fig. 227); dark brown to black in color; prosternum very slightly or not deflexed ventrally in anterior half (Fig. 219); apical maxillary palpomere weakly triangular to disc-shaped (Figs. 289 & 353) 3

4(3) Body size small, total length 2.5–4.5 mm (NOTE: *L. misellus* would key out to this couplet) … 5

- Body size large, total length 4.6–5.6 mm 13

5(4) Apical maxillary palpomere rounded to disc-shaped (Fig. 289); Apical metatarsomere nearly entirely, or entirely setose (Fig. LUTBRO10) 6

- Apical maxillary palpomere truncate at apex, at least rounded-triangular in shape (Fig. 353); Apical metatarsomere with at least 50% glabrous surface area (Fig. 334) 8

6(5) Pronotum with lateral borders expanded (Fig. 286); apical metatarsomere entirely setose (Fig. 295); length 2.5–3.2 mm; restricted to Cerro Duida in southeastern Venezuela … ***L. maldonadoi* Maier & Short**

- Pronotum with lateral borders smooth with outline of body, not expanded; apical metatarsomere entirely to partially setose (Fig. 205); length 3.0–4.5 mm 7

7(6) Elytron with distinctive rows of opposite-facing setae (Fig. 242); metatarsus and protarsus nearly completely tomentose, with bare patch on interior face (Fig. 248); Amazonian Ecuador … ***L. gimmeli* n. sp.**

- Elytron lacking distinctive rows of opposite-facing setae (Fig. 198); metatarsus and protarsus completely tomentose; Marabá, Brazil ..... ***L. browni* n. sp.**

8(5) Elytron with internal apical wing-binding patch of setae (Fig. 261); Brazil, south to Paraguay..... 9

- Internal face of elytron lacking wing-binding patch; Northern South America, Central America, and Lesser Antilles 10

9(8) Aedeagus with fused parameres posteriorly extended (Fig. 259); Paraguay ***L. guarani* n. sp.**

- Aedeagus with fused parameres short, not posteriorly extended (Fig. 229); Northern Brazil to Uruguay, Paraguay, Northern Argentina ..... ***L. germari* Grouvelle**

10. Body strongly wedge-shaped..... ***L. vestitus*-complex**

- Body ovate or weakly wedge-shaped 11

11(10) Apical metatarsomere pubescent for at least half of length when viewed dorsally (Fig. 367); parameres of aedaegus with weak crenulations at border (Fig 364) . ***L. wao* Maier & Short**

- Apical metatarsomere pubescent for significantly less than half of length when viewed dorsally (Fig. 223); parameres of aedaegus smooth, lacking weak crenulations at border (Fig 221) 12

12(11) Apical protarsomere two-toned, dark brown to nearly apex, testaceous at apex; femora light brown dorsally and dark brown ventrally; tibiae dark brown (Fig. 219); apex of parameres not extended apically (Fig. 221) ..... ***L. funkae*** **Maier & Short**

- Apical protarsomere, femora, and tibae entirely reddish-brown to testaceous (Fig. 250); apex of parameres extended apically (Fig. 252) ..... ***L. grenadensis*** **Maier & Short**

13(4) Antennae very short, not reaching anterior border of pronotum, antennomeres forming compact club (Figs. 305 & 310); highly convex body shape; apical protarsomere with only basal third tomentose (Fig. 311); Scutellum nearly twice as wide as long; Brazil .... ***L. pilula*** **Erichson**

- Antennae longer, always reaching at least anterior border of pronotum, only forming loose club (Figs. 208 & 354); body shape variable; vestiture of apical protarsomere variable; scutellum much less than twice as wide as long; northern and western South America and Central America 14

14 (13) Body size large (6.4–6.6 mm total length); elytral apex of female acuminate, produced posteriorly (Fig. 240); basal piece of male genitalia longer, 4.3 times as long as fused parameres (Fig. 237); Peru, Andes Mountains ..... … ***L. gigas*** **Hinton**

- Body size smaller (<6.0 mm total length); elytral apex of female rounded to slightly acuminate, not produced posteriorly (Figs. 297 & 312); basal piece of male genitalia shorter, less than 4.3x as long as fused parameres (Fig. 193 & 315); northern South America and Central America ... 15

15(14) Parameres of male genitalia truncate at apex, apex rectangular in shape when viewed laterally (Figs. 193 & 323); apical hind tarsomere always completely bare (Figs. 328 & 197); mountainous regions of Central America and western South America 16

- Parameres of male genitalia elongate at apex, apex strongly actute in shape when viewed laterally (Figs. 315 & 280); apical hind tarsomere variable (Figs. 283 & 274); northern South America 19

16(15) Body narrowly ovate in shape, with widest point midway down elytra (Fig. 320); humeri reduced, not at all protuberant, not projecting from outline of body; parameres not extended posteriorly (Fig. 323); Apical metatarsomere bare, basal four tarsomeres pubescent; high mountain streams in Costa Rica ..... ***L. torrens* n. sp.**

- Body wedge-shaped, with widest point near elytral humeri or at one third of the way down elytra (Figs. 339 & 297); humeri protuberant, projecting from outline of body; parameres not or extended posteriorly (Figs. 300 & 193); All metatarsomeres bare; mountainous regions of Central America and western South America 17

17(16) Apical protarsomere densely pubescent basally, becoming more sparsely pubescent apically (Fig. 346); humeri weakly protuberant (Fig. 339); apex of parameres not extended posteriorly (Fig. 357); prosternum deflexed to accommodate head; Mérida Andes, Venezuela ..... ***L. violaceus* Maier & Short**

- Apical protarsomere densely pubescent basally, evenly pubescent to apex (Fig. 196); humeri weakly or strongly protuberant (Figs. 190 & 297); apex of parameres not or extended posteriorly (Figs. 193 & 300); prosternum not deflexed to accommodate head; mountainous regions of Central America and western South America 18

18(17) Humeri strongly protuberant (Fig. 190); apex of parameres extended posteriorly (Fig. 193); Panama ..... ***L. barrae* n. sp.**

- Humeri weakly protuberant (Fig. 297); apex of parameres extended posteriorly (Fig. 300); Southern Andes – Bolivia and Southern Peru ..... ***L. montanus* Grouvelle**

19(15) Body form narrowly ovate, narrowing gently posteriorly (Fig. 312); Elytra with distinct narrow glabrous "striae" running longitudinally (Fig. 312); Andean South America, Peru and Ecuador ..... ***L. tocache* n. sp.**

- Body form broadly ovate, narrowing sharply in posterior quarter (Fig. 277); Elytra evenly clothed with setae, lacking distinct narrow glabrous "striae" running longitudinally (Fig. 277); Venezuela and the Guyanas 20

20(19) Apical protarsomere entirely glabrous (Fig.269) ..... ***L. gustafsoni* Maier & Short**

- Apical protarsomere at least partially pubescent (Fig. 211) 21

21(20) Apex of protibia of male with distinct patch of long golden setae apically (Figs. 283 & 285) ..... ***L. leeanneae* Maier & Short**.

21(20) Apex of protibia of male lacking distinct patch of long golden setae apically (Figs. 210 & 212) ..... ***L. cauraensis* Maier & Short**.

22 (1) Metaventrite with medial circular glabrous patch (Fig. 376); scutellum diamond-shaped (Fig. 374); elytron with seven rows of shallow punctures (Fig. 369); apical maxillary palpomere narrow (Fig. 375); Mérida Andes, Venezuela **[*SAXITROCHUS*]** … ***Saxitrochus meridaensis* (Maier & Short)**

- Metaventrite without medial circular glabrous patch (Fig. 67); scutellum triangular (Fig. 66);

elytral punctation dense, confused, not in rows (Figs. 59 & 105); apical maxillary palpomere wide (Fig. 62) 23

23 (22) Body size small, less than 2.0 mm total length; body covered in long, erect setae (Figs. ANDCOR1 & 56); first abdominal ventrite with four wax-filled pits (Fig. 71); South America **[*ANDOTROCHUS*]** 24

- Body size larger, greater than 2.0 mm total length; body covered in golden, apressed, scale-like setae (Figs. 92 & 99); first abdominal ventrite smooth, lacking four wax-filled pits (Fig. 111); North America and Central America **[*AURITROCHUS*]** 25

24 (23) Elytra with deep punctation (Fig. 56); hind tarsi almost completely tomentose (Fig. 72); first abdominal ventrite with four, deep, wax-filled pits (Fig. 71); Andean South America … ***Andotrochus minutus* (Maier & Short)**

- Elytra with shallow punctation (Fig. ANDCOR1); hind tarsi nearly completely glabrous (Fig. 55); first abdominal ventrite with four, shallow, wax-filled pits (Fig. 50); Sierras Pampeanas in Argentina ..... ***Andotrochus cordobensis* n. sp.**

25 (23) Body small, dark brown in color (Fig. 92); apical metatarsomere nearly completely glabrous (Fig. 94); southern Mexico and Guatemala ..... ***Auritrochus brunneus* n. sp.**

- Body larger, medium brown to metallic gold in color (Figs. 99 & 121); apical metatarsomere at least with basal half tomentose (Fig. 125) 26

26 (25) Clypeal margin straight; apical maxillary palpomere subequal in width to apical labial palpomere; Central Arizona ..... ***Auritrochus arizonicus* (Brown and Murvosh)**

- Clypeal margin curved or emarginate; apical maxillary palpomere less than ¾ width of apical labial palpomere (Figs. 112 &113); Central Arizona 27

27 (26) Prosternum not deflexed to accommodate head (Fig. 122); mandible blunt at apex (Fig. AUTLUT9); Southwestern US to Central Mexico 28

- Prosternum deflexed to accommodate head (Fig. 100); mandible acute and toothed at apex (Fig. 99); Eastern United States to Northeastern Oklahoma ..... ***Auritrochus laticeps* (Casey)**

28 (27) Mesotibia with tomentose base (Fig. 125); South-Central United States to Northern Mexico ..... ***Auritrochus luteus* (LeConte)**

- Mesotibia with glabrous base (Fig. 147); Central Mexico ..... ***Auritrochus shepardi* n. sp.**

CATALOGUE OF SPECIES

LUTROCHIDAE

Type Genus: *Lutrochus* Erichson, 1847.

Distribution: Neotropical and Nearctic Regions.

Diversity: 5 genera, 27 species.

Luctrochidae Shepard & Chaboo 2015: 163 [*lapsus calami*]

ANDOTROCHUS Maier & Short

Type Species: *Andotrochus minutus* (Maier & Short, 2013)

Andotrochus minutus (Maier & Short, 2013)

Lutrochus minutus Maier & Short 2013: 290, 301–303 (Figures 48–52), 306 (description, key, figures, distribution map)

Type Locality: El Tama National Park, Tachira State, Venezuela.

Type Deposition: MIZA (holotype).

Distribution: Venezuela (Tachira), Ecuador (Napo, Pastaza), Peru (Cusco, Amazonas).

***Andotrochus cordobensis* sp. nov.**

Type Locality: Sierra de Cordoba, Cordoba, Argentina.

Type Deposition: EMEC (holotype).

Distribution: Argentina (Cordoba).

***AURITROCHUS* Maier & Short**

Type Species: *Auritrochus luteus* (LeConte, 1852)

Auritrochus arizonicus (Brown and Murvosh, 1970)

Lutrochus arizonicus Brown and Murvosh 1970: 1031–1035 (Figures 1–3, 4–9, 10–15) (description, figures, distribution, biology, habitat notes)

Lutrochus arizonicus: Brown 1972: 22, 50 (distribution, biological information, key [in Limnichidae])

L[*utrochus*]. *arizonicus*: Bertrand 1974: 59 (biological information)

Lutrochus arizonicus: Wooldridge 1986:4 (catalog entry)

L[*utrochus*]. *arizonicus*: Brown 1987: 257 (biological information)

Lutrochus arizonensis [*lapsus calami.* Authorship misattributed to Shaeffer – confusion with *Dryops arizonensis* (Schaeffer)]: Nelson & Bellamy 1991: 1017 (outgroup in phylogeny)

Lutrochus arizonicus: Spangler et. al 2001: 160 (checklist entry)

Lutrochus arizonensis [*lapsus calami*]: Richards & Rogers 2006: 171 (habitat and distributional information)

Lutrochus arizonensis [*lapsus calami*]: Hallan 2015 (checklist entry)

Type Locality: West Clear Creek, southeast of Camp Verde, Yavapai County, Arizona, USA

Type Deposition: OMNH (holotype)

Distribution: USA (AZ)

***Auritrochus brunneus* sp. nov.**

Type Locality: Rio La Palma, Veracruz, Mexico.

Type Deposition: CNIN (holotype).

Distribution: Mexico (Veracruz).

Auritrochus laticeps (Casey, 1893)

Lutrochus laticeps: Henshaw 1885 [actual publication date apparently post-1893 – attributed name to Casey 1893]: 17 (checklist entry)

Lutrochus laticeps Casey 1893: 580 (description, key)

Lutrochus laticeps: Grouvelle 1896: 17 (key, identification notes)

[*Lutrochus*] *laticeps*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *laticeps*: Leng 1920: 185 (checklist entry)

Lutrochus laticeps: Brown and Murvosh 1970: 1030 (checklist entry)

Lutrochus laticeps: Brown 1972: 22, 51 (distribution, biological information, key [in Limnichidae])

L[*utrochus*]. *laticeps*: Bertrand 1974: 59 (biological information)

Lutrochus laticeps: Pennington 1985: 221 (distribution)

Lutrochus laticeps: Wooldridge 1986:5 (catalog entry)

Lutrochus laticeps: Brown 1987: 257 (biological information)

Lutrochus laticeps: Fink & Downer 1988: 76 (population density in Lake Erie, habitat information)

Lutrochus laticeps: Roughley and Larson 1991: 133 (distributional notes)

Lutrochus laticeps: Patrick 1996: 402 (substrate preferences)

Lutrochus laticeps: Barbour et al. 1999: B-21 (pollution tolerance values)

Lutrochus laticeps: Spangler et. al 2001: 160 (checklist entry)

Lutrochus laticeps: Barton 2004: 512 (distribution information, population density [in Elmidae?])

Lutrochus laticeps: Ratti & Barton 2006: 611 (distributional notes)

Lutrochus laticeps: Bowles et al. 2007: 117 (pollution tolerance values)

Lutrochus laticeps: Hallan 2015 (checklist entry)

Type Locality: Michigan, USA

Type Deposition: USNM [Casey Collection] (holotype).

Distribution: USA (AL, AR, DC, IL, IN, KS, MD, MI, MO, OH, MS, OK, PA, TN, WI, WV), Canada (Ontario)

Auritrochus luteus (LeConte, 1852)

Lutrochus luteus LeConte 1852: 42 (description, distribution [described in Parnidae])

Lutrochus luteus: Henshaw 1882: 230 (catalog entry)

Lutrochus luteus: Grouvelle 1896: 17 (key, identification notes)

[*Lutrochus*] *luteus*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *luteus*: Leng 1920: 185 (checklist entry)

L[*utrochus*]. *luteus* Bertrand 1956: 102–104 (biological information, larval morphology, distribution)

Lutrochus luteus: Brown 1956: 38 (distribution)

Lutrochus luteus: Sanderson & Brown 1959: 68, 70 (distribution, biological information)

Lutrochus luteus: Brown 1966: 17 (biological information)

Lutrochus luteus: Brown and Murvosh 1970: 1030 (checklist entry)

L[*utrochus*]. *luteus* Bertrand 1974: 59 (biological information)

Lutrochus luteus: Reisen 1975: 27 (ecological data, distribution)

Lutrochus luteus: Brown 1972: 22, 51 (Figure 117) (distribution, biological information, illustration, key [in Limnichidae])

Lutrochus luteus: Brown 1973: 280, 281, 284 (biological information, life history data, larval rearing)

Lutrochus luteus: Reisen 1977: 185–190 (ecological data, biological information, distribution [in Limnichidae])

Lutrochus luteus: Wooldridge 1986:5 (catalog entry)

L[*utrochus*]. *luteus*: Brown 1987: 257 (biological information)

L[*utrochus*]. *luteus*: Brown 1991: 397-399 (biological information, larval description)

Lutrochus luteus: Spangler et. al 2001: 160 (checklist entry)

Lutrochus luteus: Hallan 2015 (checklist entry)

Type Locality: Fort Gates [Gatesville], Coryell County, Texas, USA.

Type Deposition: MCZ [LeConte Collection] (holotype).

Distribution: USA (NM, OK, TX)

***Auritrochus shepardi* sp. nov.**

Type Locality: Arroyo El Platano, Querétaro, Mexico.

Type Deposition: CNIN (holotype).

Distribution: Mexico (Querétaro).

***BEROTROCHUS* Maier & Short**

Type Species: *Berotrochus geniculatus* (Chevrolat, 1864)

Berotrochus geniculatus (Chevrolat, 1864)

Lutochrus [*lapsus calami*] *geniculatus* Chevrolat 1864: 406

Lutrochus geniculatus: Grouvelle 1896: 17 (key)

[*Lutrochus*] *geniculatus*: Zaitzev 1908: 8 (checklist entry)

Lutrochus geniculatus: Darlington 1936: 75 (first record from Haiti, habitat information)

[*Lutrochus*] *geniculatus*: Blackwelder 1944: 273 (checklist entry)

Lutochrus [*lapsus calami*] *geniculatus*: Bertrand 1956: 102–104 (biological information, larval morphology, distribution, comparative notes)

Lutrochus geniculatus: Spangler et. al 2001: 160 (checklist entry)

Lutrochus geniculatus: Perez-Galabert 2008: 99 (checklist entry)

Type Locality: Cuba

Type Deposition: MNHN (lectotype) [ex. Grouvelle collection]

Distribution: West Indies: Cuba, Haiti

***LUTROCHUS* Erichson, 1847:509**

Lutochrus: Grouvelle 1889 [*lapsus calami*]

Lutochrus: Chevrolat 1864 [*lapsus calami*]

Lutrochous: Zaitzev 1908: 8 [*lapsus calami*] (checklist entry)

Lutochrus: Darlington 1939 [*lapsus calami*]

Lutrochous: Hinton 1935:173 [*lapsus calami*]

Neolutrochus Hinton 1939b:180 [*nomen nudum*] **syn. nov.**

Lutochrus [*lapsus calami*] Bertrand 1956: 100 (Figure I:1), 102–104 (biological information, larval morphology, figure, distribution, comparative notes)

Lutochrus [*lapsus calami*] Bertrand 1967: 130–131(Figure 6) (biological information, larval morphology, figure)

Lutochrus [*lapsus calami*] Bertrand 1974: 59 (biological information)

Type Species: *Lutrochus pilula* Erichson.

BYRRHOMORPHUS Sharp, 1882:125

Byrrhomorphus: Zaitzev 1908: 8 (checklist entry)

Lutrochus: Blackwelder 1944: 273 (checklist entry)

Byrrhomorphus: Blackwelder 1944: 273 (checklist entry)

Lutrochus: Roughley and Larson 1991: 133 (distributional notes)

Lutrochus: Brown 1965: 227 (habitat and biological information)

Lutrochus: Brown 1976: 22, 23, 51, 52, 57 (distribution, biological information, key, illustrations of adults and larvae [in Limnichidae])

Lutrochus: Brown 1987: 253–254, 257, 261–262, 266–267 (biological information, habitat)

Lutrochus: Spangler et. al 2001: 151, 160 (checklist entry)

Lutrochus: Maier 2013: 66

Lutrochus acuminatus Grouvelle, 1889

Lutochrus [*lapsus calami*] *acuminatus* Grouvelle 1889:163, pl. 6 (description, figure)

Lutrochus acuminatus: Grouvelle 1896: 17 (key)

[*Lutrochus*] *acuminatus*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *acuminatus*: Blackwelder 1944: 273 (checklist entry)

Lutrochus acuminatus: Spangler et. al 2001: 160 (checklist entry)

Lutrochus acuminatus: Maier & Short 2013: 285–290, 292 (Figures 8–13), 306 (redescription, lectotype designation, key, figures, distribution map, habitat photos)

Lutrochus acuminatus: Maier 2013: 71 (habitat notes)

Type Locality: Colonia Tovar, Aragua State, Venezuela.

Type Deposition: MNHN (lectotype).

Distribution: Venezuela (Aragua, Trujillo)

Lutrochus cauraensis Maier & Short, 2013

Lutrochus cauraensis Maier & Short 2013: 289–290, 293 (Figs, 14–19), 306 (description, key, figures, distribution map)

Lutrochus cauraensis: Maier 2013: 85 (habitat notes)

Type Locality: Kanarakuni, Alto Caura, Bolívar State, Venezuela.

Type Deposition: MIZA (holotype).

Distribution: Venezuela (Bolívar)

Lutrochus funkae Maier & Short, 2014

Lutrochus funkae Maier & Short 2014: 59 (Fig. 1), 60–62 (Figs. 3–6), 70 (description, key, figures, distribution map)

Type Locality: Moco Moco River, near Lethem, Guyana.

Type Deposition: USNM (holotype).

Distribution: Guyana (Rupununi)

Lutrochus germari Grouvelle, 1889

Lutochrus [*lapsus calami*] *germari* Grouvelle 1889: 163 (description)

Lutrochus germari Grouvelle 1896: 17 (diagnostic notes, key)

[*Lutrochus*] *germari*: Zaitzev1908: 8 (checklist entry)

L[*utrochus*]. *germari*: Hinton 1939a: 24 (diagnostic notes)

Neolutrochus braziliensis Hinton 1939b:180 [*nomen nudum*] **syn. nov.**

[*Lutrochus*] *germari*: Blackwelder 1944: 273 (checklist entry)

Lutrochus germari: Costa et. al 1996: 47–56 (redescription and illustration of adult, description and illustrations of larva and pupa, biology and distribution in Brazil)

Lutrochus germari: Spangler et. al 2001: 160 (checklist entry)

Lutrochus germari: Valente-Neto and Fonseca-Gessner 2011: 683–686 (detailed bionomic study of larvae and habitat description)

Lutrochus germari: Maier & Short 2013: 285, 306 (habitat notes)

Type Locality: Teresópolis, Rio de Janiero, Brazil.

Type Deposition: MNHN (lectotype) [ex. Grouvelle collection]

Distribution: Brazil

Lutrochus gigas Hinton, 1939a

Lutrochus gigas Hinton 1939a: 23–24 (description, illustration of adult, comparative notes [described in Limnichidae])

Lutrochus gigas Grouv[elle]. Hinton 1939a: 24. [Hinton noted specimens with labels bearing this identification, but no record of a published name]

[*Lutrochus*] *gigas*: Blackwelder 1944: 273 (checklist entry)

Lutrochus gigas: Spangler et. al 2001: 160 (checklist entry)

Lutrochus gigas: Maier & Short 2013: 285, 306

Lutrochus gigas: Shepard & Chaboo 2015: 164 (Distribution & biological notes).

Type Locality: Vilcanota [Mountain range or river?], Perú

Type Deposition: BMNH (holotype, male) [ex. Kraatz collection from the SDEI "Deutsches Entomologisches Institut Berlin-Dahlem"]

Distribution: Perú

Lutrochus grenadensis Maier & Short, 2014

Lutrochus grenadensis Maier & Short 2014: 59 (Fig. 1), 62–65 (Figs. 7–11), 70 (description, key, figures, distribution map).

Lutrochus grenadaensis [lapsus calami] Maier & Short 2014: 60 & 62.

Type Locality: Mont Plaisr River, Grenada.

Type Deposition: OMNH (holotype).

Distribution: West Indies: Grenada

Lutrochus gustafsoni Maier & Short, 2013

Lutrochus gustafsoni Maier & Short 2013: 290–291, 294 (Figures 20–26), 306 (description, key, figures, distribution map)

Type Locality: Culebra, north of Cerro Duida, Amazonas State, Venezuela.

Type Deposition: MIZA (holotype).

Distribution: Venezuela (Amazonas)

Lutrochus leeanneae Maier & Short, 2014

Lutrochus leeanneae Maier & Short 2014: 59 (Fig. 1), 65–68 (Figs. 12–17), 70 (description, key, figures, distribution map)

Type Locality: Kasikasima, Suriname.

Type Deposition: NZCS (holotype).

Distribution: Suriname

Lutrochus maldonadoi Maier & Short, 2013

Lutrochus maldonadoi Maier & Short 2013: 290, 297–299 (Figures 34–39), 306 (description, key, figures, distribution map)

Type Locality: Culebra, north of Cerro Duida, Amazonas State, Venezuela.

Type Deposition: MIZA (holotype).

Distribution: Venezuela (Amazonas)

Lutrochus misellus Grouvelle, 1896

Lutrochus misellus Grouvelle 1896: 17 (description, key)

[*Lutrochus*] *misellus*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *misellus*: Blackwelder 1944: 273 (checklist entry)

Lutrochus misellus: Spangler et. al 2001: 160 (checklist entry)

Type Locality: Nouveau Fribourg [Nova Friburgo], Rio de Janiero, Brazil

Type Deposition: NMHN [not there – must be somewhere else in the collection]

Distribution: Brazil

Lutrochus montanus Grouvelle, 1896

Lutrochus montanus Grouvelle 1896: 16–17 (description, key)

[*Lutrochus*] *montanus*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *montanus*: Blackwelder 1944: 273 (checklist entry)

Lutochrus [*lapsus calami*] *montanus* Bertrand 1956: 102–104 (biological information, larval morphology, distribution, comparative notes)

Lutrochus montanus: Spangler et. al 2001: 160 (checklist entry)

Type Locality: Yungos de Cochabamba, [State?], Bolivia

Type Deposition: NMHN

Distribution: Bolivia

Lutrochus pilula Erichson, 1847

Lutrochus pilula Erichson 1847: 509–510 (description)

[*Lutrochus*] *pilula*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *pilula*: Blackwelder 1944: 273 (checklist entry)

Parnus pilula [attributed to Germar]*:* Wooldridge 1986:4 (catalog entry)

Lutrochus pilula: Spangler et. al 2001: 160 (checklist entry)

Lutrochus pilula: Maier & Short 2013: 306

Type Locality: Brazil

Type Deposition: ZMHB (2 syntypes)

Distribution: Brazil

Lutrochus vestitus (Sharp, 1882)

Byrrhomorphus vestitus Sharp 1882: 126 (description, comparative notes [described in Parnidae])

[*Byrrhomorphus*] *vestitus*: Zaitzev 1908: 8 (checklist entry)

[*Lutrochus*] *vestitus*: Hinton 1935: 173 (synonymy of *Byrrhomorphus* with *Lutrochus*)

[*Lutrochus*] *vestitus*: Blackwelder 1944: 273 (checklist entry)

Lutrochus vestitus: Spangler et. al 2001: 160 (checklist entry)

Lutrochus vestitus: Maier & Short 2013: 288, 290, 295–297 (Figures 27–33), 306 (redescription, key, figures, distribution map, habitat photos)

Lutrochus vestitus: Maier 2013: 49 (habitat notes)

Type Locality: Panimá, El Quiché, Guatemala.

Type Deposition: BMNH (holotype [Champion collection]).

Distribution: Guatemala, Venezuela (Barinas, Falcón, Sucre, Aragua, Bolívar), French Guiana.

Lutrochus violaceus Maier & Short, 2013

Lutrochus violaceus Maier & Short 2013: 290, 304–306 (Figures 55–60) (description, key, figures, distribution map, habitat photos)

Type Locality North of Ejido, Rt. 4 river crossing, Mérida State, Venezuela.

Type Deposition: MIZA (holotype)

Distribution: Venezuela (Mérida)

Lutrochus wao Maier & Short, 2014

Lutrochus wao Maier & Short 2014: 59 (Fig. 1 & 2), 68–70 (Figs. 19–23), 70 (description, key, figures, distribution map)

Type Locality: Parabara, Guyana.

Type Deposition: CBDUG (holotype).

Distribution: Guyana, French Guiana

SAXITROCHUS Maier & Short

Saxitrochus meridaensis (Maier & Short, 2013)

Lutrochus meridaensis Maier & Short 2013: 290, 299–301 (Figures 40–47), 306 (description, key, figures, distribution map, habitat photos)

Type Locality: Cascada velo de la Novia, Mérida State, Venezuela.

Type Deposition: MIZA (holotype).

Distribution: Venezuela (Mérida)

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APPENDIX I:

CHARACTERS AND CHARACTER STATES USED IN MORPHOLOGICAL ANALYSIS

Abdomen

0. Apical abdominal ventrite

0. Rounded

1. Notched

2. Acute

3. With two notches

The shape of the abdominal ventrite. Within Lutrochidae, states 0,1 and 2 are most common.

1. Lateral first abdominal ventrite plateaus

0. Present

1. Absent

The first abdominal ventrite in most Lutrochidae possesses a small, roundish flattened area laterally on the same plane of the metepisternum.

2. Metatarsal rests on First Abdominal Ventrite

0. Absent

1. Present

The presence of defined metatarsal rests, or depressions, delineated by a carina on the first abdominal ventrite. The character state is present in many members of the outgroup and a few *Lutrochus* species.

3. Number of Abdominal Ventrites Connate

0. Two

1. Three

2. Four

The number of basal abdominal ventrites that are immovably fused. All Lutrochidae have two connate ventrites.

Antenna

4. Antennal Apical Sensillum

0. Present

1. Absent

This character is defined as the presence of a small campaniform sensillum at the apex of the eleventh antennomere.

5. Antennal Groove

0. Absent

1. Strong

2. Weak

3. Weak, only at posterior border

Defined as the presence and strength of a groove and carina on the gena, which allows for reception of the antennae when the antenna is tucked under the head. The derived states are found only in the Lutrochidae, with varying degrees of definition across the family.

6. 2nd segment of antenna expanded

0. Absent

1. Present

Second antennomere expanded to accommodate the following antennomeres. The derived character state is restricted to the Dryopidae.

7. Antennal length

0. Short

1. Medium

2. Long

The length of the antenna from base to apex. Long is defined as reaching past anterior border of pronotum, medium as just reaching the anterior border of the pronotum, and short as not at all reaching the anterior border of the pronotum.

Elytron

8. Apical wing-binding patch

0. Absent

1. Present

The apical wing-binding patch is a small area of curved setae or hooks near the apex of the elytron on the interior surface. The derived state is found only in a group of southern and central South American *Lutrochus*.

9. Elytral epipleuron

0. Narrow

1. Wide, well developed

The width of the ventral face of the elytral epipleuron. The derived state is found only in a single species – *Lutrochus acuminatus*.

10. Elytral humeri, interior view

0. Acute

1. Rounded

2. Obtuse

The shape of the humeral angle of the elytron, as viewed from the interior of the elytron.

11. Elytral punctures

0. Fine

1. Very Coarse

2. Coarse

Defined as the coarseness of the overall elytral punctation. Fine punctures are (>5μm) across, very coarse punctation (<10 μm), and coarse punctation (5-10 μm).

12. Elytral striae

0. Complete furrows

1. Strongly punctate

2. Weakly Punctate

3. Visible in "shadow"

4. Invisible

This character refers to the strength and presence of the elytral striae. Often the striae are not complete furrows, but instead are made up of varying degrees of punctation. The striae, while not visible on some pinned specimens, become visible in the translucent cuticle of cleared specimens, “in the shadow.”

13. Elytral sutural interior longitudinal depression

0. Absent

1. Present

On the elytron at the elytral suture, several species of dryopoids possess a longitudinal indentation or depression, hypothesized to be a form of elytral locking mechanism.

16. Lateral interior elytral carina

0. Broken

1. Continuous

The condition of a short elytral carina on the median edge of the elytron.

17. Scutellar border of elytra

0. Crenulate

1. Serrate

2. Smooth

The sculpture of the elytral edge, laterad of the scutellum.

18. Sutural elytral puncture row

0. Present, well developed

1. Present, weak

2. Absent

The derived state is defined as a reduction in the strength and depth of the elytral stria immediately laterad to the the elytral suture. The stria may be reduced to a series of shallow punctures (State 1), or completely absent (State 2).

Male Genitalia

19. Fusion of Parameres

0. Absent

1. Present, partially fused

2. Present, entirely fused

The parameres of the male genitalia are completely separated in the plesiomorphic state. The parameres are fused to varying degrees in the apomorphic states (States 1 and 2).

Habitus

20. Body shape

0. Ovate

1. Obovate

2. Wedge-shaped

3. Elongate

The overall shape of the body in dorsal habitus view.

21. Hydrofuge tomentum

0. Present

1. Absent

The hydrofuge tomentum (State 0) is a dense coating of specialized setae. These setae are not modified in such a way that they give the surface of the beetle a shimmery appearance. This is in contrast to a dense coat of setae that give the beetle a furry appearance (State 1).

22. Legs

0. Unmodified, cursorial

1. Modified, fossorial

The apomorphic state (State 1) is defined as all legs having some modification for digging. The legs in this state are often expanded, with teeth or spines.

23. Pubescence Length

0. Short

1. Medium

2. Long

This character is defined as the length of the overall dorsal pilosity of the body.

24. Tibial Spurs

0. Normal

1. Enlarged

This character refers to the general shape of the tibial spurs on all legs. Only members of the outgroup (*Heterocerus* sp. and *Ceradryops* sp.) have enlarged tibial spurs (State 1), likely modified for digging.

25. Total Body Length

0. Small (>3.0 mm)

1. Medium (3.1-4.5 mm)

2. Large (4.6-6.0 mm)

This character refers to the total length of the body, measured longitudinally, from head to tip of abdomen.

Head

26. Clypeus exending ventrally below antennae

0. Length less than or equal to the width of antennifer

1. Length greater than the width of antennifer

The clypeal length is the distance from the frontocylpeal suture to the clypeolabral suture. It uses the width of an antennifer as a reference. The derived character state (State 1), is found in *Auritrochus* spp.

27. Epicranial suture

0. Absent

1. Present, weak, Y-shaped

2. Present, strong, Y-shaped, with weak spot at center of frons

The epicranial suture is a Y-shaped suture between the frons and the apex of the head. The derived state is only present in a lineages of Lutrochidae, and may be so prominent that it appears as a weak spot that is nearly translucent.

28. Interfacetal Setae Length

0. Short, or absent

1. Long

This character refers to the length of the interfacetal setae, present only in Lutrochidae and a few outgroup taxa. Taxa which lack interfacetal setae are coded as 0. This character is *not* independent from Character 27 (Interfacetal Setae).

29. Interfacetal Setae

0. Absent

1. Present

The interfacetal setae are setae with arise between the ommatidia of the compound eye. Among the taxa included in this analysis, the derived state (State 1) is found only in Lutrochidae and several species of Dryopidae.

30. Occipital Border of Head

0. Straight

1. Bisinuate

2.With Square Notch

This character refers to the shape of the occipital border of the head near the vertex. The border may be bisinuate or straight (States 0 or 1), or may have a slight, square-shaped emargination (State 2).

31. Occipital Longitudinal Notch or Line

0. Absent

1. Present, as notch

2. Present, as line

This character refers to the shape of the occipital suture. In Lutrochidae, the suture is reduced to a small notch (State 1) or line (State 2), or is completely absent (State 0).

32. Stridulatory patches of the head

0. Absent

1. Present

This character refers to the presence of two small patches of transverse striations at the vertex of the head, hypothesized to be used for stridulation. The derived state (State 1) is only present in two species of Lutrochidae.

33. Transverse Occipital Ridge

0. Absent

1. Slight, change in setal pattern at ridge

2. Present, with distinct ridge

The transverse occipital ridge is a weak, but distinct transverse ridge near the vertex of the head. The ridge may be very weak, indicated only a slight change in the setation posterior to the ridge (State 1), or may be strong, with a dictinct cuticular ridge (State 2).

Mesothorax

34. Apical mesotibial excavation

0. Absent

1. Present, lacking strong carina

2. Present, with strong carina

This character refers to the apex of the mesotibia, and whether it has an excavation for reception of the mesotarsus (States 1 & 2).

35. Rugose patch apically on interior margin of mesotibia

0. Absent

1. Present

The derived character state (State 1) is an autapomorphy of a single species of Peruvian *Lutrochus* and refers to the presence of a small patch of rugosity near the apex of the mesotibia.

36. Meso- and Meta- ventrites immovably fused

0. Absent

1. Present

The derived character state (State 1) represents the fusion of the meso- and meta-ventrites, in the plesiomorphic state (State 0), the meso- and metaventrites are moveably articulated. The derived state is a potential synapomorphy which unites Dryopidae.

37. Mesocoxal rests on metaventrite

0. Absent

1. Present, shallow

2. Present, deep

This character refers to the depressions present on the metaventrite, which accommodate the posterior border of the mesocoxae The depressions, if present, may be shallow (State 1) or deep (State 2). The derived states are most often seen in the wood-inhabiting species, presumably these character states to allow the beetle to fit into tighter spaces.

38. Mesocoxal separation

0. Narrow

1. Wide

2. Very wide

A narrow separation (State 0) of the mesocoxae is defined as a space between the mesocoxae less than 1x as wide as the mesocoxa. Wide (State 1) is defined as a space between the mesocoxae 1-1.5x as wide as the mesocoxa. Very wide (State 2) is defined as a space between the mesocoxae 1.5-2x as wide as the mesocoxa.

39. Mesocoxal spine

0. Absent

1. Weak

2. Prominent

This character refers to the presence of a spinose process on the internal face of the mesocoxa.

40. Mesoventral Fossa

0. Absent

1. Present, Transverse

2. Present, Longitudinal

The mesoventral fossa is a small depression on ventrite located medially on the ventrite for reception of the prosternal process. This space may be transverse (State 1) or longitudinal (State 2).

41. Mesotibial excavational process

0. Absent

1. Weak

2. Strong

This character refers to the presence of a distinct process (States 1 & 2) surrounding the apical mesotibial excavation (Character 32).

42. Mesotibial expansion

0. Present

1. Absent

Refers to the apical expansion of the mesotibia adjacent to the apical mesotibial excavation.

Metathorax

43. Dorsal Surface of Metatibia

0. Straight

1. Convex

Refers to the shape of the metatibia on the dorsal surface. The metatibia may be straight (State 0) or convex (State 1).

44. Metacoxal cavity depression

0. Absent

1. Present

The presence of a distinct depression on the mesotibia

45. Metacoxal lateral process

0. Absent

1. Present

This character refers to the presence (State 1) of a small hooked process on the lateral border of the metacoxa. This character is only visible in dissection.

46. Metacoxal medial spinose process

0. Absent

1. Present, spiny

2. Present, rounded

The metacoxal medial spinose process is a small projection on the medial border of the coxa.

47. Metacoxal Plates

0. Well-Developed

1. Weakly-Developed

2. Absent

This character refers to the development of the metacoxal plates (expansion of the metacoxa over the metatibia) – the metacoxal plate may be well-developed (State 0), weakly-developed (State 1), or absent (State 2).

48. Metacoxal posterior border

0. Straight

1. Slightly curved

2. With weak process

3. With strong process

This character refers to the shape of the posterior border of the metacoxa. This border may be straight, lacking a process (State 0), angled, with a spinose process (State 2 & 3), or with a rounded process (State 1).

49. Metaventral Bare Patch

0. Absent

1. Present

This character is an autapomorphic character of the species *Saxitrochus meridaensis* and refers to the distinctive glabrous patch on the disc of the metaventrite.

50. Metaventral diamond-shaped sulcus

0. Absent

1. Present

The metaventral diamond-shaped sulcus is a small depression and separation of the ventrite located medially on the ventrite.

51. Metaventral Transverse Suture

0. Well Developed

1. Obscured Laterally - more than ½

2. Absent

3. Obscured Laterally - less than ½

This character refers to the transverse suture of the metaventrite, located in the posterior 1/3 of the ventrite. It may be well-developed (State 0), absent (State 2), or obscured or invisible along some portion of its length (States 1 & 3).

52. Metatarsal vestiture

0. Glabrous

1. Tomentose

2. Tomentose, apical tarsomere glabrous

3. Tomentose, apical 3/4 of apical tarsomere glabrous

The metatarsal vestiture refers to the degree of pilosity present on the metatarsi. This character is particularly important at the species level.

53. Metatibial cleaning fringe

0. Absent

1. Present – long

2. Present – short

This character refers to the presence and length of a "cleaning fringe" or tomentum on the metatibia. This patch of slightly longer setae is hypothesized to be used for grooming the plastron setae.

54. Metatibial Vestiture

0. Glabrous

1. Tomentose, with narrow bare patch

2. Tomentose to apical 1/16th, with narrow bare patch

3. Tomentose

The metatarsal vestiture refers to the degree of pilosity present on the metatibia. This character is particularly important at the species level.

55. Metatrochanter shape

0. Rounded

1. Acute

2. Spinose

3. Curved spinose

4. Flat

This character refers to the shape of the metatrocanter and whether it is excavated to receive the apical edge of the metatibia. If excavated (States 1-4), the trochanter will have a slight process or spine.

56. Metendosternite shape

1. Rectangular, wide

2. Rectangular, narrow

3. V-shaped

4. Trapezoidal Triangular

The shape of the metendosternite varies across species, and the structure may be seen in a cleared specimen.

57. Post-mesocoxal lines

0. Present - lines distinctly separate from mesocoxal cavities

1. Absent - lines not distinctly separate from mesocoxal cavities

The post-mesocoxal lines are located just behind the mesocoxae, if present (State 0). The lines may be completely reduced and no separate from the mesocoxal cavities.

58. Posterior edge of coxal excavation

0. Separate metaventral transverse suture

1. Confluent with metaventral transverse suture

The derived state (State 1) is a putative synapomorphy uniting the clade of *Auritrochus* and *Saxitrochus*, and is defined as the post-metacoxal lines being convergent with the metaventral transverse suture.

59. Postmetacoxal pores

0. Absent

1. Present

This character state (State 1) is only present in *Andotrochus*, and is the presence of two deep pores behind each of the metacoxae, located on the first abdominal ventrite. These pores are filled with setae and a waxy substance, and are potentially used for sensing or for grooming the plastron.

60. Sparse setae on the metatibia

0. Absent

1. Present

This character refers to the presence of several longer, sparse setae on the metatibia. NOTE: metatibiae with the apomorphic state (State 0), may be completely covered in pilosity, but with no longer, distinctive setae. The derived state (State 1) is characteristic of Dryopidae and Heteroceridae.

Mouthparts

61. Apical labial palpomere

0. Cylindrical Expanded

1. Apically Vase shaped

2. Expanded Apically, slightly sinuate

3. Strongly, distinctly truncate

This character refers to the shape of the apical palpomere of the labial palps.

62. Apical maxillary palpomere shape

0. Cylindrical, tapered at apex

1. Expanded at apex

The derived state (State 1) is shared among all Lutrochidae and varies slightly (See character 72). The derived state is also present in the laraine elmid genus *Phanocerus*.

63. Clypeolabral suture

0. Straight

1. Weakly concave

2. Strongly concave or notched

This character refers to the shape of the suture between the clypeus and the labrum. The suture is more strongly curved in *Auritrochus* spp.

64. Clypeus expanded, covering part of labrum

0. Absent

1. Present

The derived character state (State 1) refers to a distal expansion of the clypeus, which obscures a portion of the labrum. This character state is only present in outgroup taxa.

65. Fronto-clypeal suture visibility

0. Visible

1. Not Visible

This character refers to the visibility of the fronto-clypeal suture, and whether it is obscured on the cuticular surface. The derived state (State 1) unites Lutrochidae and Dryopidae.

66. Labral transverse row of setae

0. Absent

1. Present

The labral transverse row of setae is a row of closely-spaced, long setae (1/2 the length of the labrum) present 2/3 of the way up the labrum on *Saxitrochus meridaensis*.

67. Mandibular apex

0. Well Developed

1. Reduced

This character refers to the development of the apical shearing surface of the mandible. The mandible in most species is acute, with a variety of teeth, but in the derived state (State 1), this surface is blunt and reduced.

68. Mandibular Mola

0. Present, well developed

1. Present, weak

2. Absent

The mandibular mola is the chewing surface of the mandible, and it may be well-developed (State 0), with chewing adaptations, or it may be reduced (State 2), and lacking grinding structures.

70. Mandibular shape

0. Long, falciform

1. Stout, securiform, robust

This character refers to the shape and conformation of the mandible. Falciform mandibles (State 0) are common in *Auritrochus*, while securiform mandibles (State 1) are more prevalent in *Lutrochus*.

71. Mandibular teeth

0. One

1. Two

2. Three

3. Four

4. With two lamellae

5. Five

The number mandibular teeth refers to the shape of the apex of the mandibles and whether they have teeth or flattened, stacked, lamellate-like teeth (State 4), as seen in some *Auritrochus* species.

74. Prostheca partly well-sclerotized

0. Absent

1. Present

The prostheca is the membranous extension on the interior face of the mandible. In Dryopidae, the prostheca is partially sclerotized (State 1).

72. Maxillary apical palpomere shape

0. Flat

1. Triangle

2. Circular, discoid

3. Cylindrical

4. Rounded Triangle

This character varies widely across Lutrochidae, with all Lutrochidae possessing expanded apical maxillary palpomeres (States 0, 1, 2, 4).

73.Maxillary apical sensilla

0. Present

1. Absent

The maxillary apical sensilla is a small patch of setose sensillae present at the apex of the most distal maxillary palpomere.

75. Subapical maxillary sensilla

0. Absent

1. Present – single

2. Present – Patch

The maxillary subapical sensilla is a small campaniform sensilla, present (State 1) on the apical palpomere of the maxillary palp, alternatively, a small patch of sensillae may be present in the same area (State 2).

Prothorax

76. Anterior border of scutellum

0. Straight

1. Concave

2. Triangularly produced

3. Convex

This character refers to the shape of the anterior border of the scutellum. State 3 (triangularly produced) is when the anterior border of the scutellum is angled, so that the overall shape of the scutellum is diamond-shaped.

77. Anterior pronotal carina

0. Absent

1. Present

The anterior pronotal carina (State 1) is a transverse carina bordering the anterior margin of the pronotum.

78. First Protarsal Segment Vestiture

0. Glabrous

1. Entirely Tomentose

2. Apical 3/4 Glabrous

3. Dorsally glabrous / Ventally tomentose

The pilosity of the first tarsomere of the protarsus varies greatly among species, and is an excellent diagnostic character for delimiting species. The first tarsomere may be anywhere from entirely glabrous (State 0) to entirely tomentose (State 1).

79. Prosternal Apophysis

0. Absent

1. In front of midline

2. At midline

This character refers to the transverse invagination of cuticle across the center of the prosternum.

80. Lateral Pronotal Carinae

0. Present

1. Inconspicuous

2. Absent

The lateral pronotal carinae in Byrrhoidea may be present and conspicuous, with a distinct bead (State 0), inconspicuous, with a partial or no bead (State 1), or absent (State 2).

81. Oblique carina of the hypomeron

0. Present, across half-way point

1. Absent

2. Present, across apical 1/3

This character refers to an oblique carina across the hypomeron – this is associated with a shallow excavation for reception of the forelegs, and may be present and positioned at different points along the hypomeron. In *Lutrochus acuminatus*, the carina is slightly anterior relative to the carina's position on other species of *Lutrochus*.

82. Posterior coxal carina (Procoxae)

0. Present, complete

1. Present, incomplete

2. Absent

The posterior coxal carina is a carina present (States 0 & 1) on the posterior face of the procoxa, visible only when the specimen is dissected.

83. Prescutellar dimples

0. Present

1. Absent

The prescutellar dimples are two shallow pits on the pronotum immediately anterior to the scutellum.

84. Prescutum texture

0. Smooth

1. Rugose

The prescutum which immediately preceeds the scutellum is rugose (State 1) in all but a couple of outgroup taxa (*Phanocerus* sp. and *Heterocerus* sp.). In these taxa it is completely smooth (State 0).

85. Profemur

0. Narrow – not expanded.

1. Wide – expanded.

The profemur may be expanded (State 1), where the femur is approximately ¼ as wide as long, or not expanded (State 0), where the femur is approximately 1/5 as wide as long.

86. Pronotal antennal pockets

0. Absent

1. Present

The pronotal antennal pockets are small, shallow excavations in the hypomeron of the pronotum for reception of the apex of the antennae. This character is most prevalent in the Limnichidae.

87. Pronotal prescutellar notch

0. Absent

1. Present, shallow

2. Present, deep

This character is only visible on dissected specimens. The derived states (States 1 & 2) indicated the presence of a narrow sclerotized arch visible on the internal face of the pronotum directly anterior to the scutellum. The arch is present (States 1 & 2) in all species of Lutrochidae, except those members of the genus *Lutrochus*.

88. Pronotum Sublateral Carinae

0. Absent

1. Present

The sublateral carinae of the pronotum are a set of shallow carinae present (State 1) just mesad of the lateral border of the pronotum. The derived state (State 1) is only present in the outgroups.

89. Prosternal Fold

0. Absent

1. Present

State 1 of this character is defined as the presence of a transverse fold in the prosternum, which causes the anterior edge of the prosternum to point ventrally. *Lutrochus acuminatus* displays this character state.

90. Prosternal process shape

0. acute, with central process

1. truncate

2. rounded

3. acute

The shape of the apex of the prosternum varies widely across Byrrhoidea, but remains relatively constant in Lutrochidae. Notable exceptions are in *L. maldonadoi*, which has a rounded process (State 2), and *N. geniculatus*, which possesses an acutely angled process (State 3).

91. Prosternal process touching metaventrite

0. Absent

1. Present

The derived state of this character (State 1) indicates that the prosternal process touches the metaventrite – this is only possible when the mesoventrite is reduced medially.

92. Prosternal process width

0. Narrow

1. Wide

The prosternal process may be narrow (State 0) or wide (State 1). State 1 is defined as the prosternum nearly as long as wide, with width measured at the widest point and length starting at the anterior edge of the procoxae. State 0 is anything narrower than State 1.

94. Prosternum length

0. Long

1. Short

This is the length of the prosternum in front of the procoxae. Short is less than the width or the prcoxae, Long is longer than width of procoxae.

95. Protarsal Length

0. Short

1. Long

The length of the protarsi (all tarsomeres combined) is variable among species and is useful for delimiting species within Lutrochidae. Longer tarsi are prevalent in species of *Auritrochus*.

96. Protarsal rests on prosternum

0. Absent

1. Present

The derived character state (State 1) indicates the presence of shallow excavations in the prosternum for reception of the profemora. This state may represent an adaptation for a life in confined spaces.

97. Protibial dorsal edge

0. Straight

1. Strongly Convex

2. Weakly convex

3. Weakly convex, with indentation at apical 1/3

The dorsal edge of the protibia varies greatly among species of Lutrochidae, and is useful for determining species delimitation.

98. Protibial longitudinal carina

0. Absent

1. Present

The derived state (State 1) is the presence of a longitudinal carina along the length of the protibia, for reception of the protarsus. This state may represent an adaptation for a life in confined spaces. Within Byrrhoidea, it is only found among species of Lutrochidae.

99. Protrochanter excavation

0. Absent

1. Present

The derived character state (State 1) is the presence of an excavation in the protrochanter for reception of the protibia when leg is folded. This state may represent an adaptation for a life in confined spaces.

102. Anterior Processes of the Mesoprescutum

0. Blunt

1. Curved

These processes are present at the anterio-lateral corners of the mesoprescutum, and may extend longer than the length of the mesoprescutum. These may be blunt at the apex (State 0) or curved (State 1).

103. Prosternum and pronotum extended anteriorly "Turtleneck"

0. Absent

1. Present

This character is defined as the expansion (State 1) of the anterior border of the prosternum and pronotum to accommodate the head, giving the head a "Turtleneck" appearance.

Wing

104. Anal Cell

0. Present

1. Absent

The derived state (State 1) represents a reduction in the venation of the anal cell of the hind wing.

105. Radial Cell

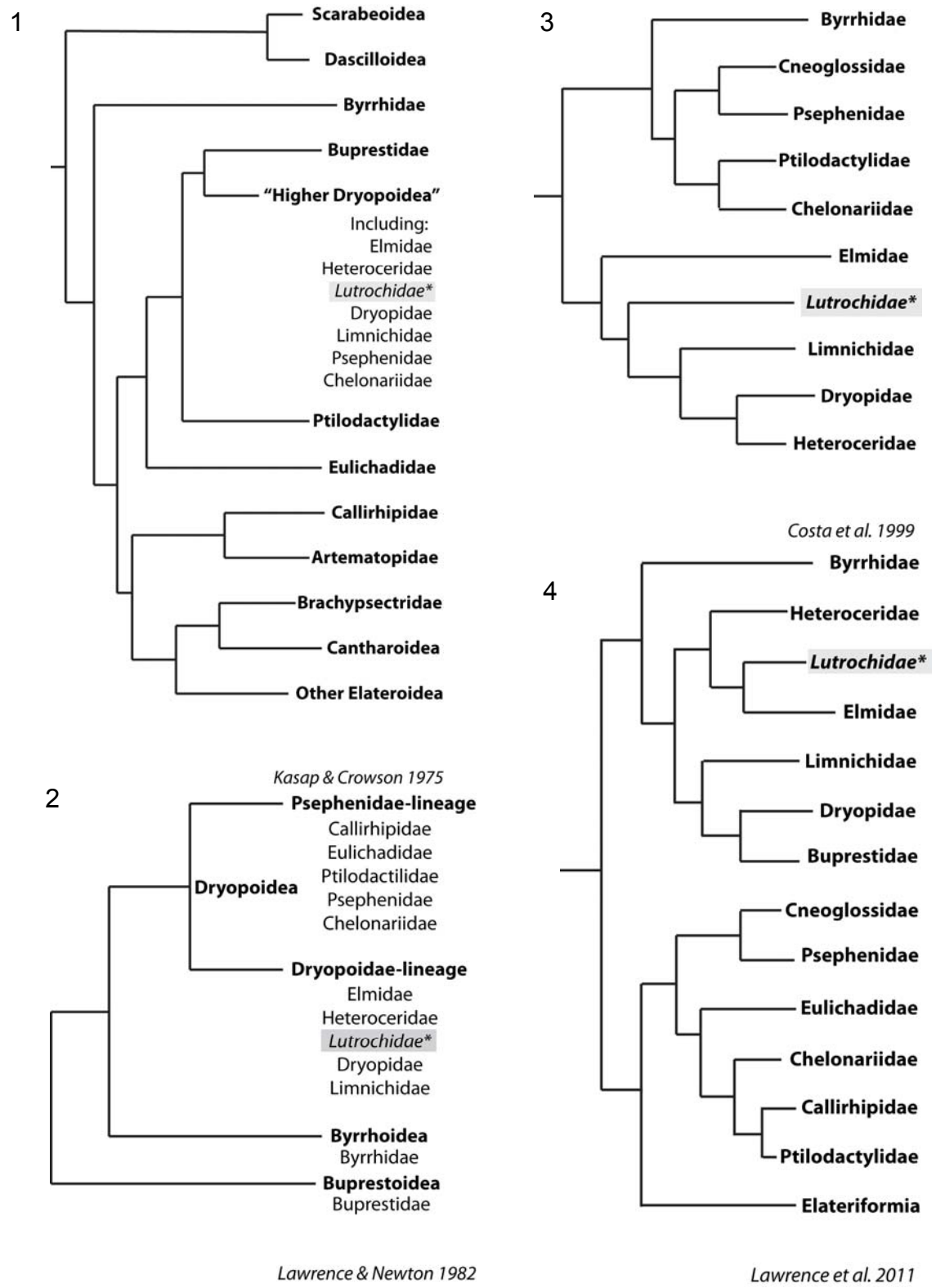
0. Present

1. Absent

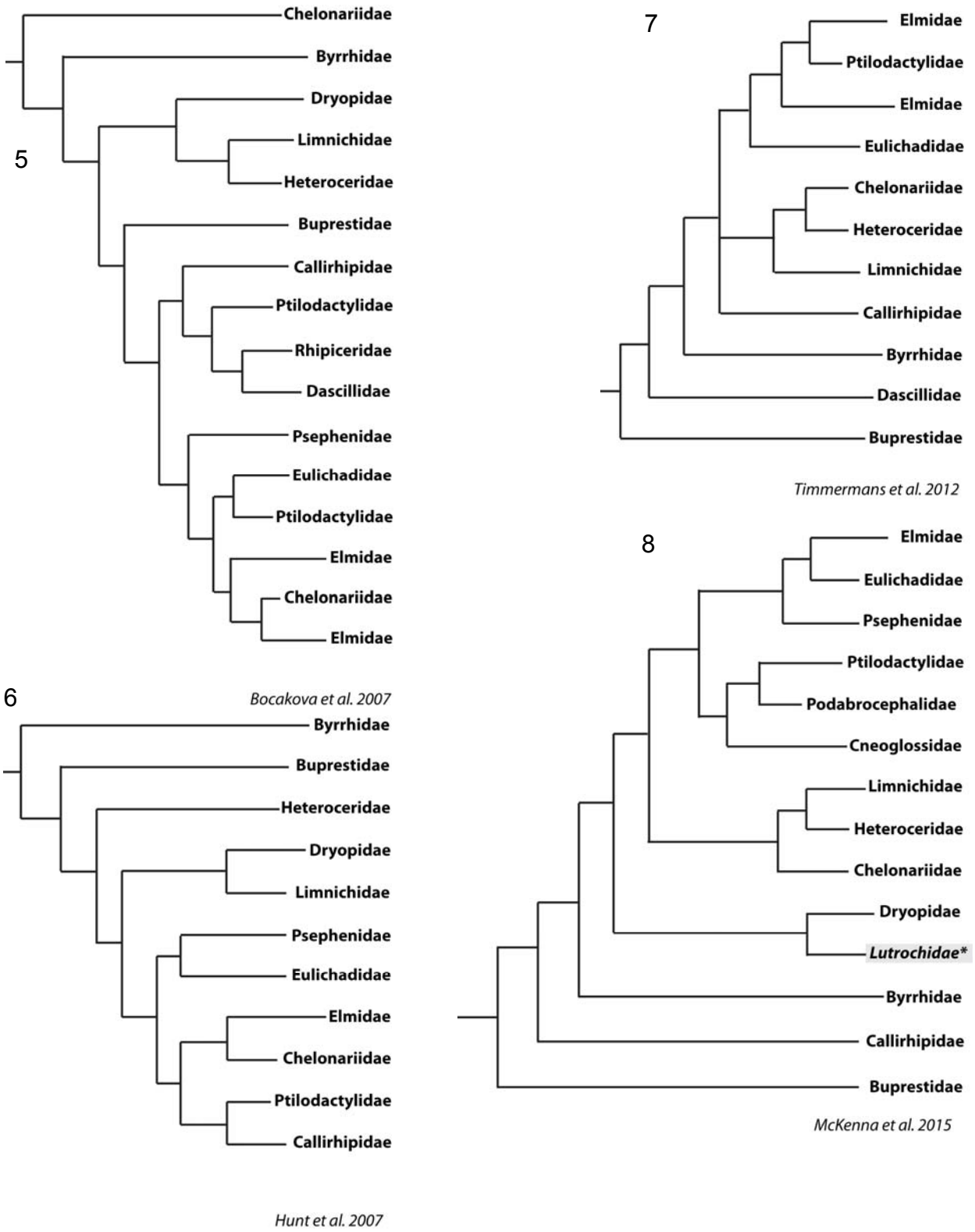
The derived state (State 1) represents a reduction in the venation of the radial cell of the hind wing.

APPENDIX II:

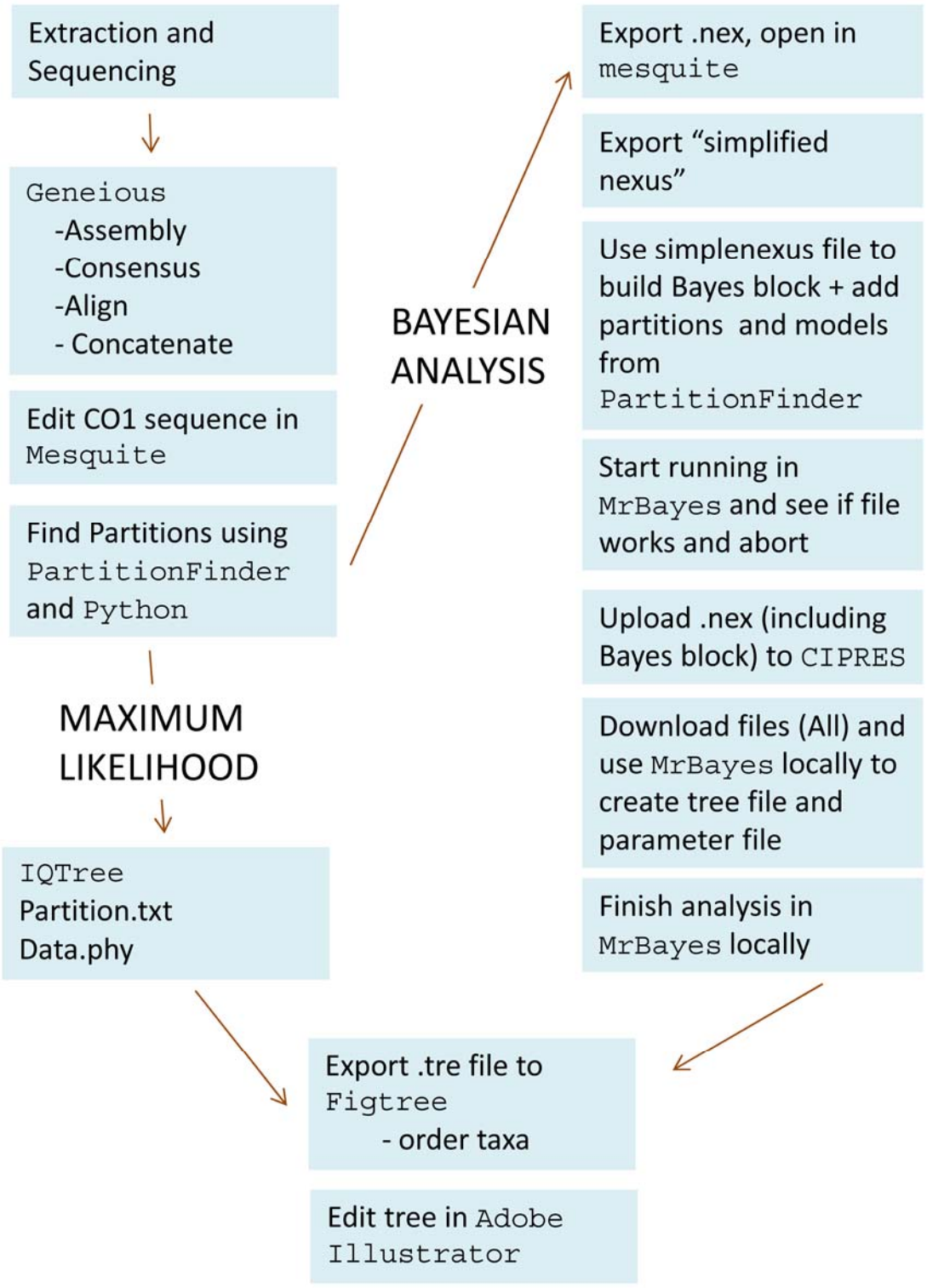
FIGURES



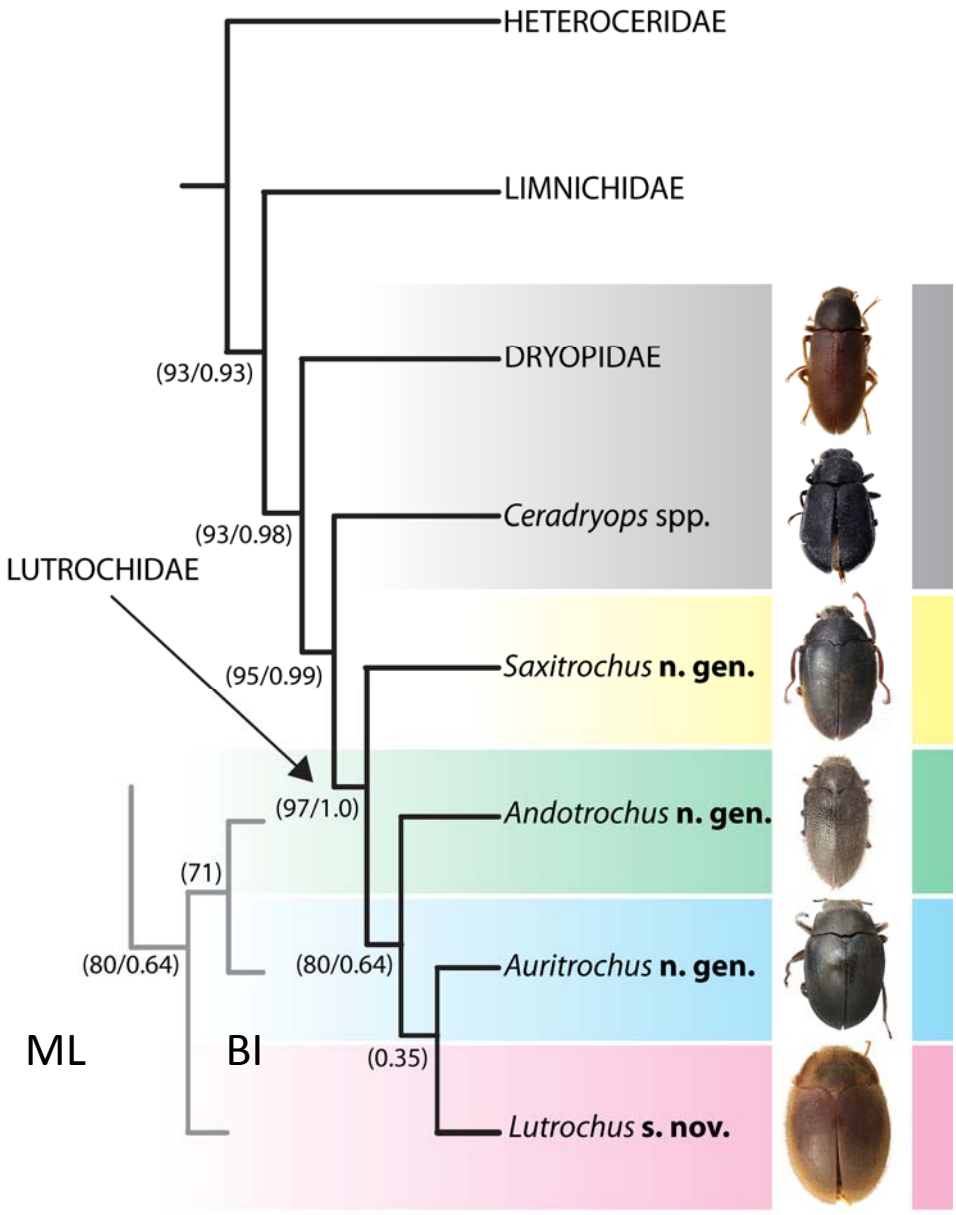
Previous hypotheses of evolution in Byrrhoidea. 1. After Kasap & Crowson (1975) based on morphological data. 2. After Lawrence & Newton (1982), based on morphological data. 3. After Costa et al. (1999), based on morphological data. 4. After Lawrence et al (2011), based on morphological data.



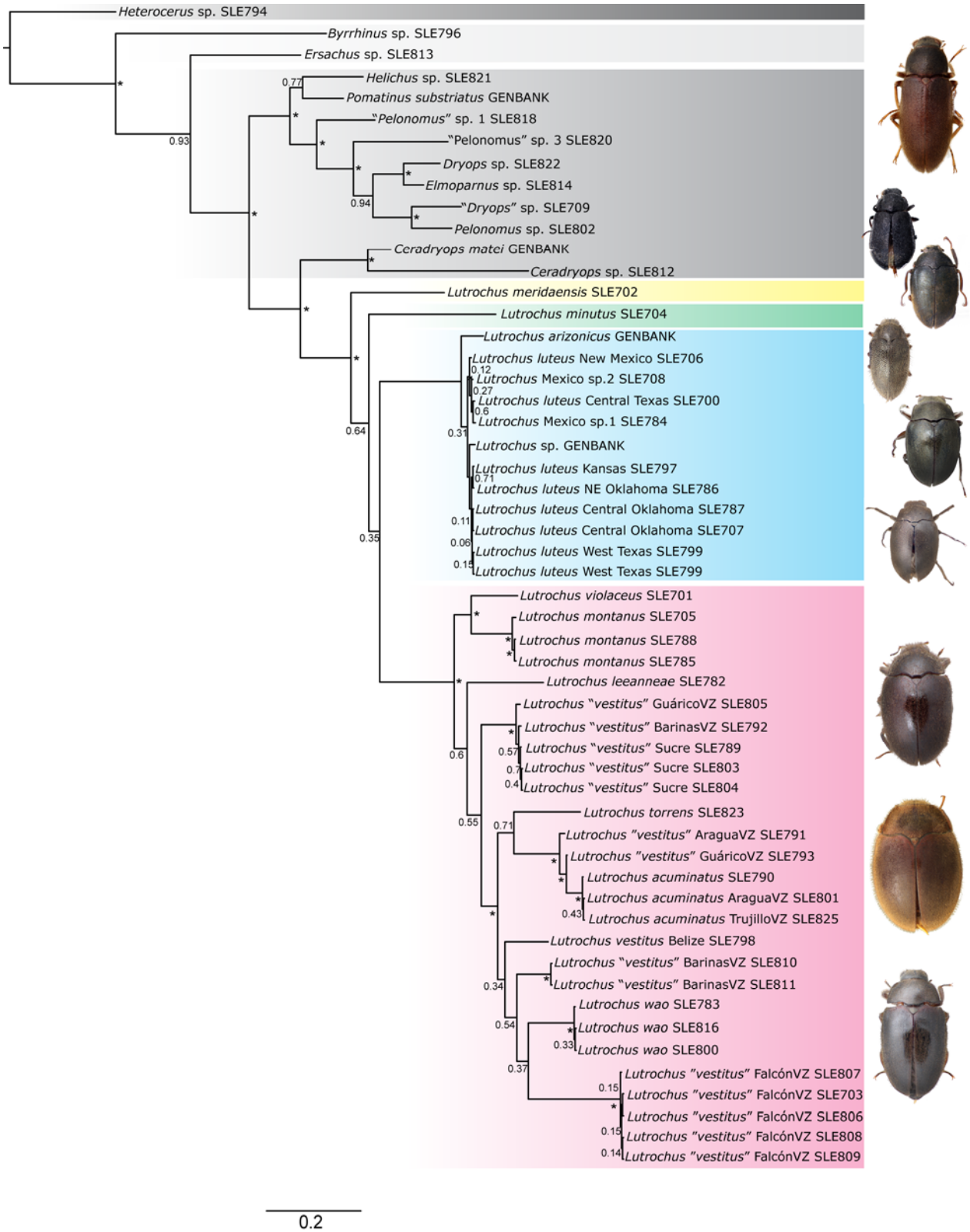
Previous hypotheses of evolution in Byrrhoidea. 5. After Bocakova et al. (2007) based on 18S, 28S, 16S, and COI. 6. After Hunt et al. (2007), 18S, 16S, and COI. 7. After Timmermans et al. (2012), based on mitochondrial genomic data. 8. After McKenna et al. (2015), based on 8 nuclear genes and 6 nuclear protein-coding genes.



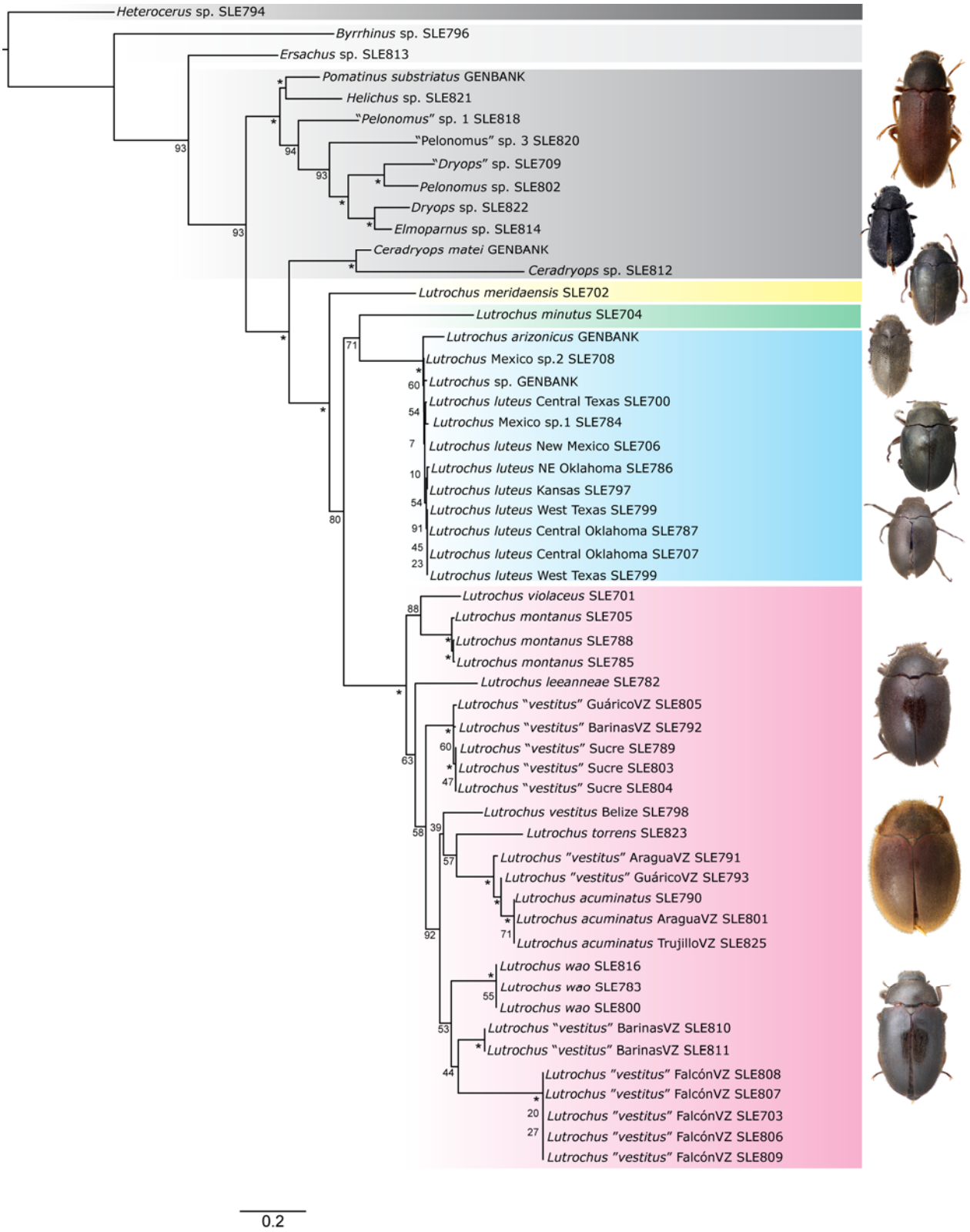
9. Standard workflow for molecular phylogenetic analysis of Lutrochidae from extraction to final phylogenetic tree. Methods included both Bayesian Inference and Maximum Likelihood methods.



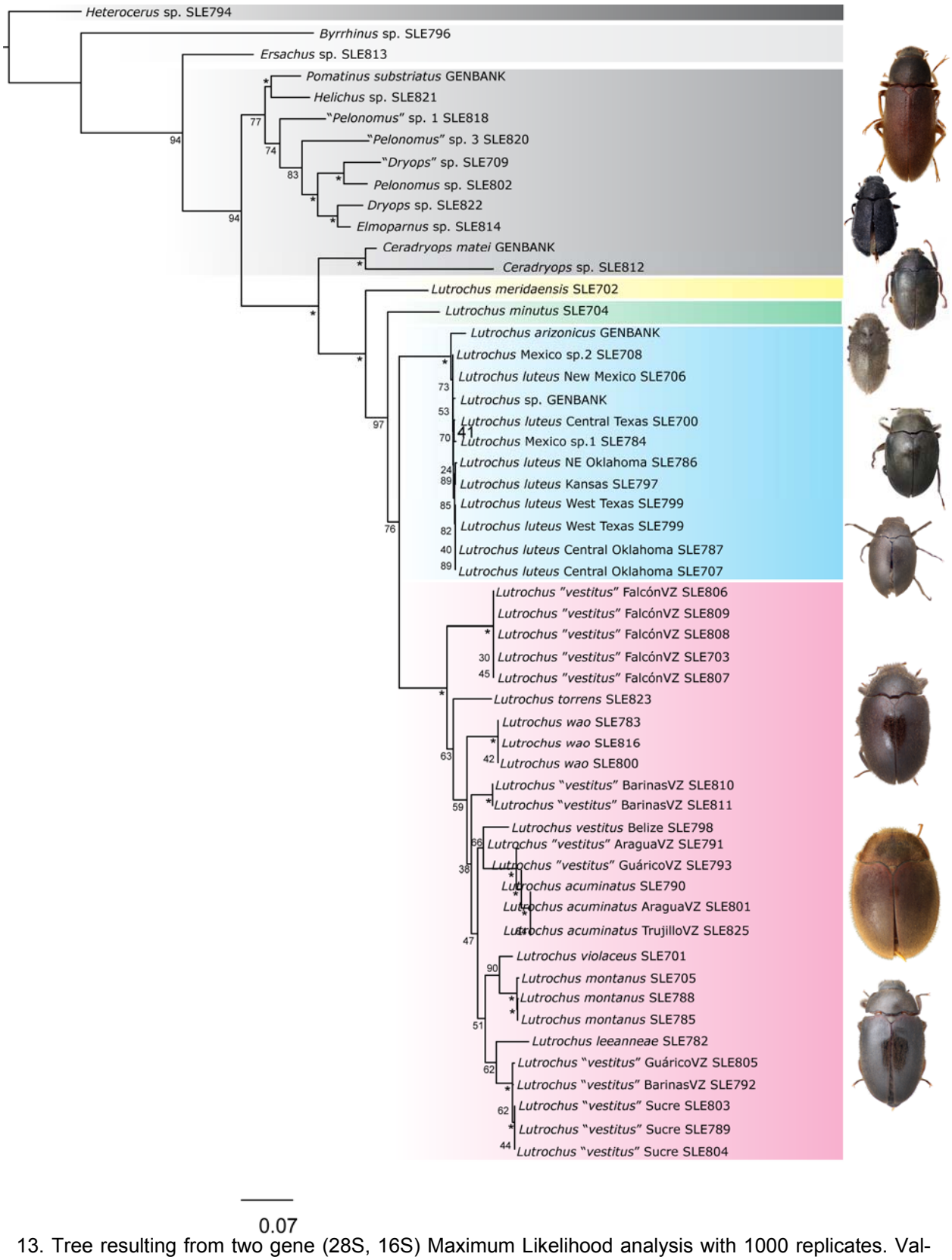
10. Simplified version of Three-gene (28S, 16S, COI) phylogenetic trees generated using Bayesian Analysis and Maximum Likelihood Analysis. Bootstrap support values and posterior probabilities are given in parentheses at nodes of the trees. Incongruent results for the placement of *Andotrochus* in ML analysis are presented in gray in inset.



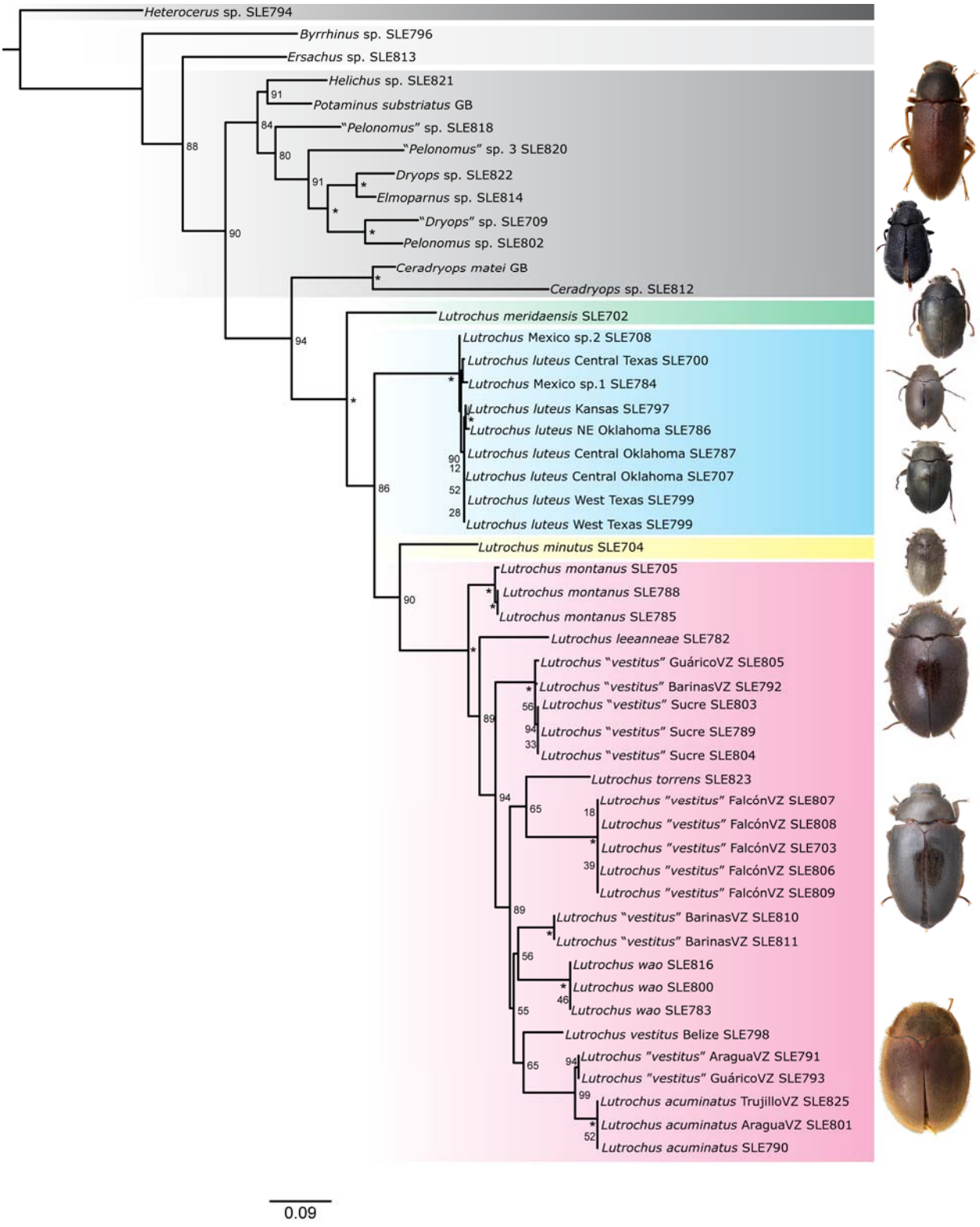
11. Tree resulting from three-gene (28S, 16S, COI) Bayesian analysis with 30 million generations at 50% burn-in. Values at nodes indicate posterior probabilities. Nodes with significant support (>0.95 PP) are indicated with an asterisk.



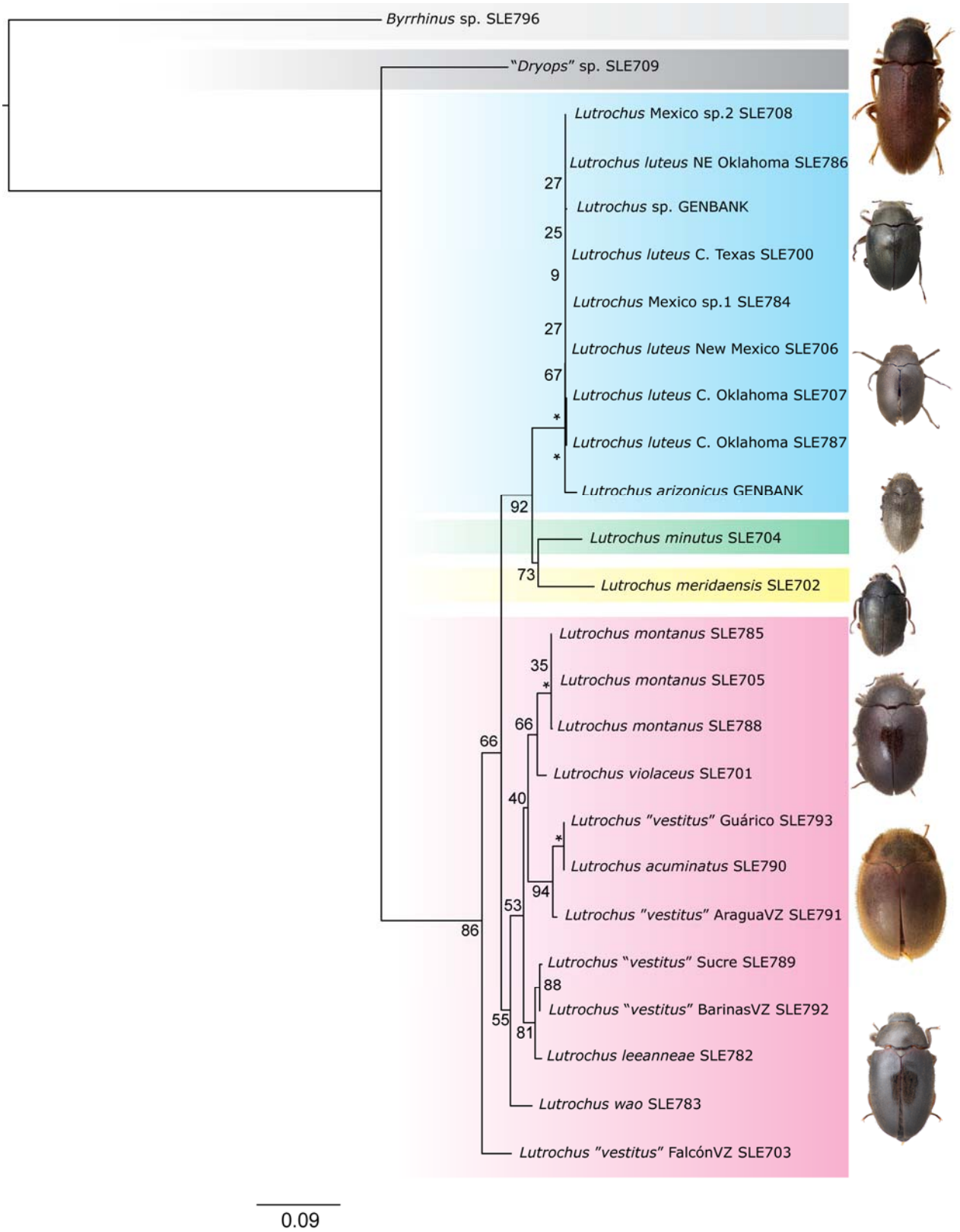
12. Tree resulting from three-gene (28S, 16S, COI) Maximum Likelihood analysis with 1000 replicates. Values at nodes indicate posterior probabilities. Nodes with bootstrap support values above 95 are indicated with an asterisk.



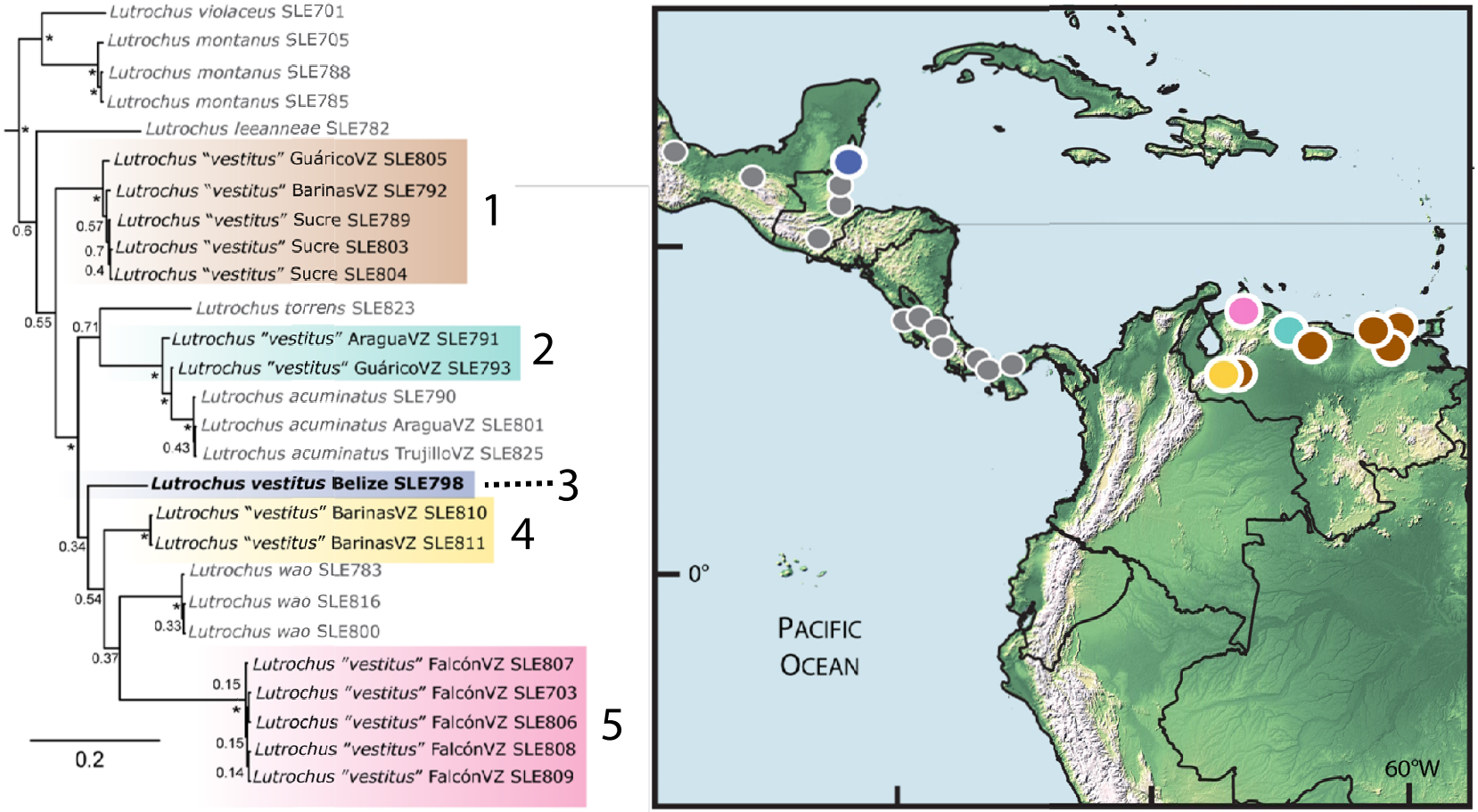
13. Tree resulting from two gene (28S, 16S) Maximum Likelihood analysis with 1000 replicates. Values at nodes indicate posterior probabilities. Nodes with bootstrap support values above 95 are indicated with an asterisk.



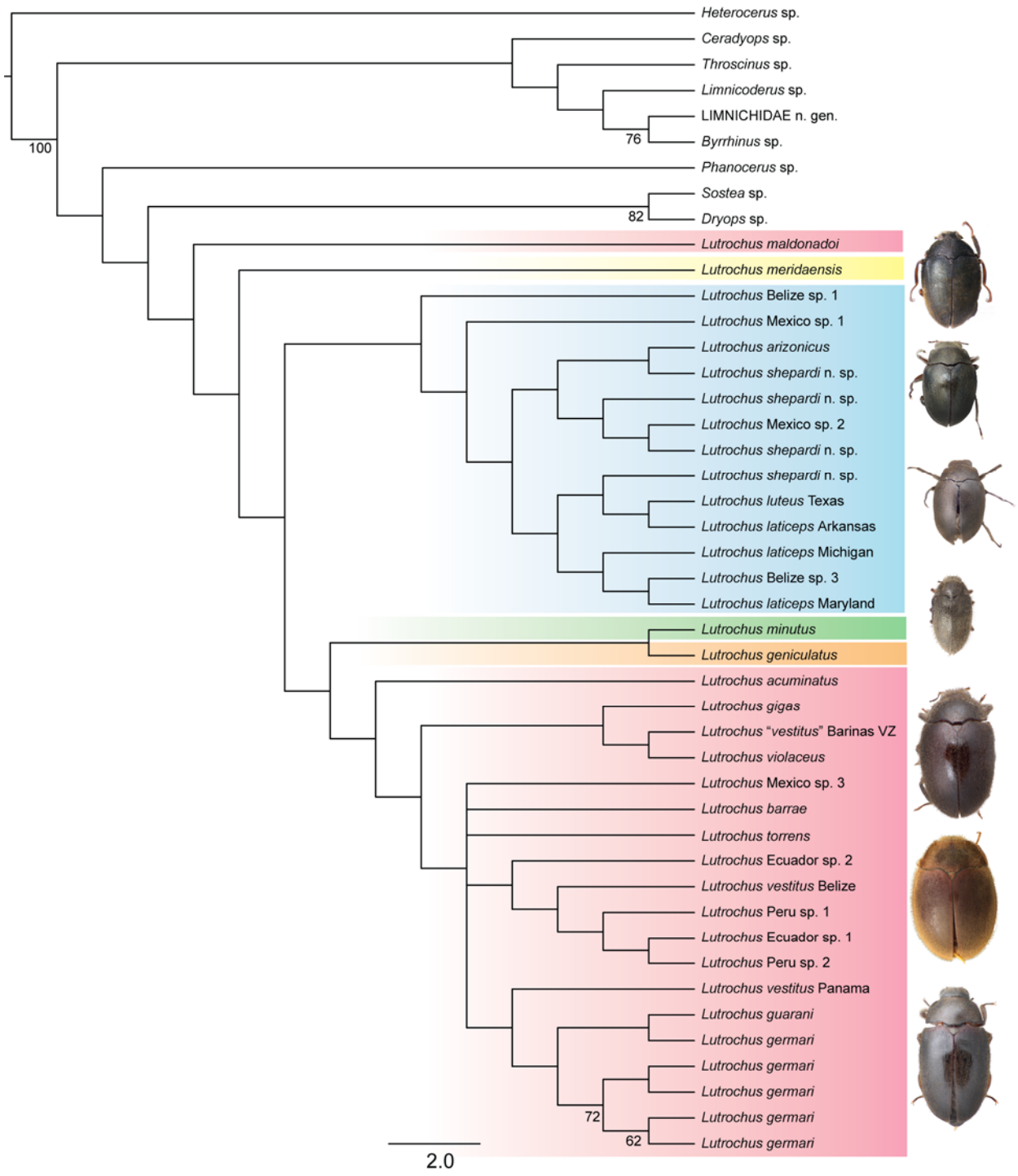
14. Tree resulting from single gene (16S) Maximum Likelihood analysis with 1000 replicates. Values at nodes indicate posterior probabilities. Nodes with bootstrap support values above 95 are indicated with an asterisk.



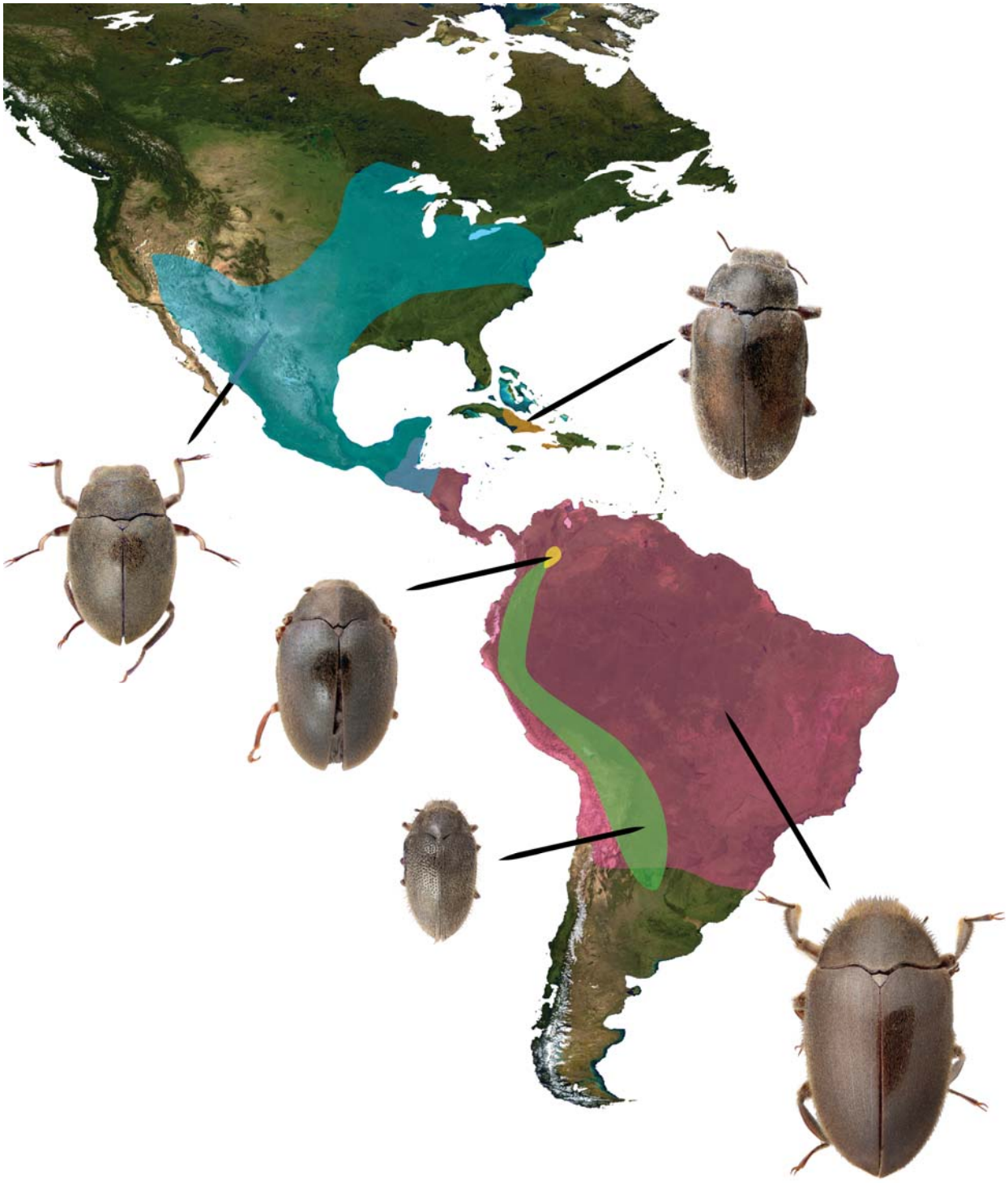
15. Tree resulting from single gene (28S) Maximum Likelihood analysis with 1000 replicates. Values at nodes indicate posterior probabilities. Nodes with bootstrap support values above 95 are indicated with an asterisk.



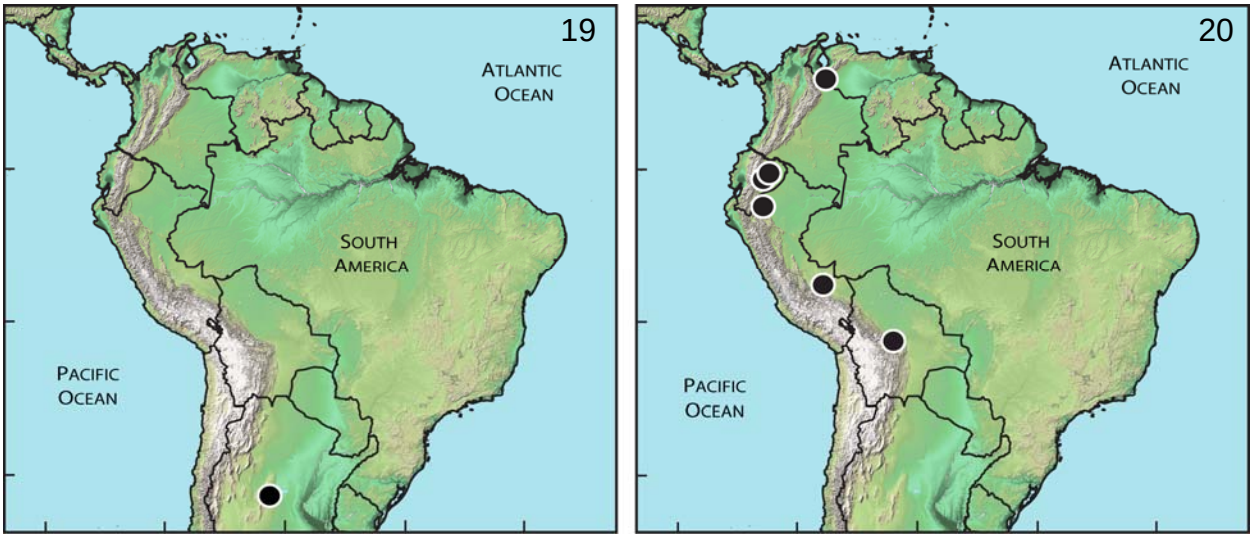
16. Branch of *Lutrochus* s. str. from free resulting from three-gene (28S, 16S, COI) Bayesian analysis with 30 million generations at 50% burn-in. Sequences from specimens morphologically indistinguishable from *Lutrochus vestitus* are highlighted on the tree. True *Lutrochus vestitus* is highlighted in bold. Branches in the Lutrochus "vestitus-group" are numbered for ease of reference. Colored dots on the map correspond to branches *Lutrochus "vestitus"* on the tree.



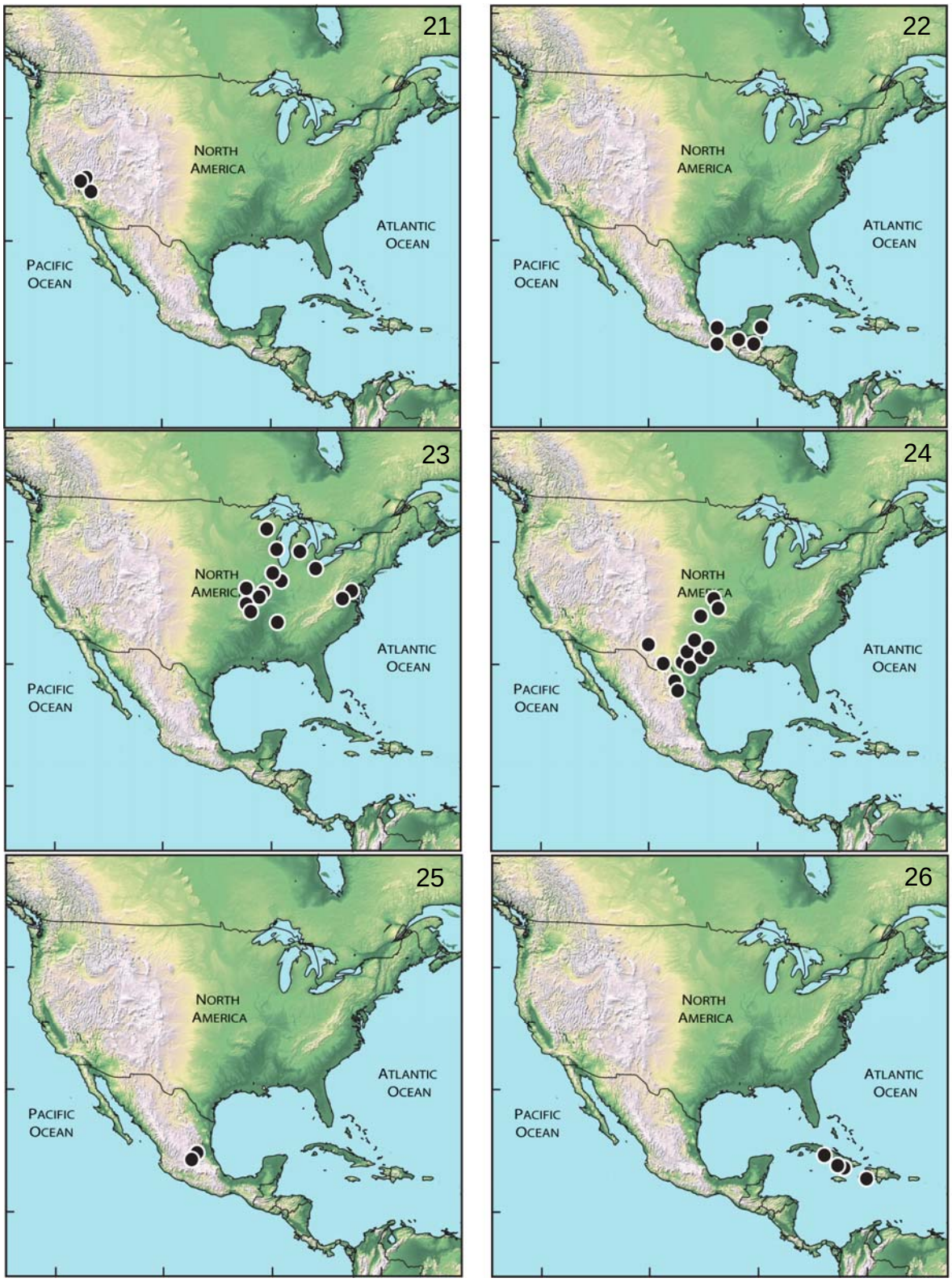
17. Strict consensus of four most parsimonious trees recovered by New Technology Search with 10 initially added sequences in TNT. Bootstrap support values of greater than 50 are indicated on the tree.



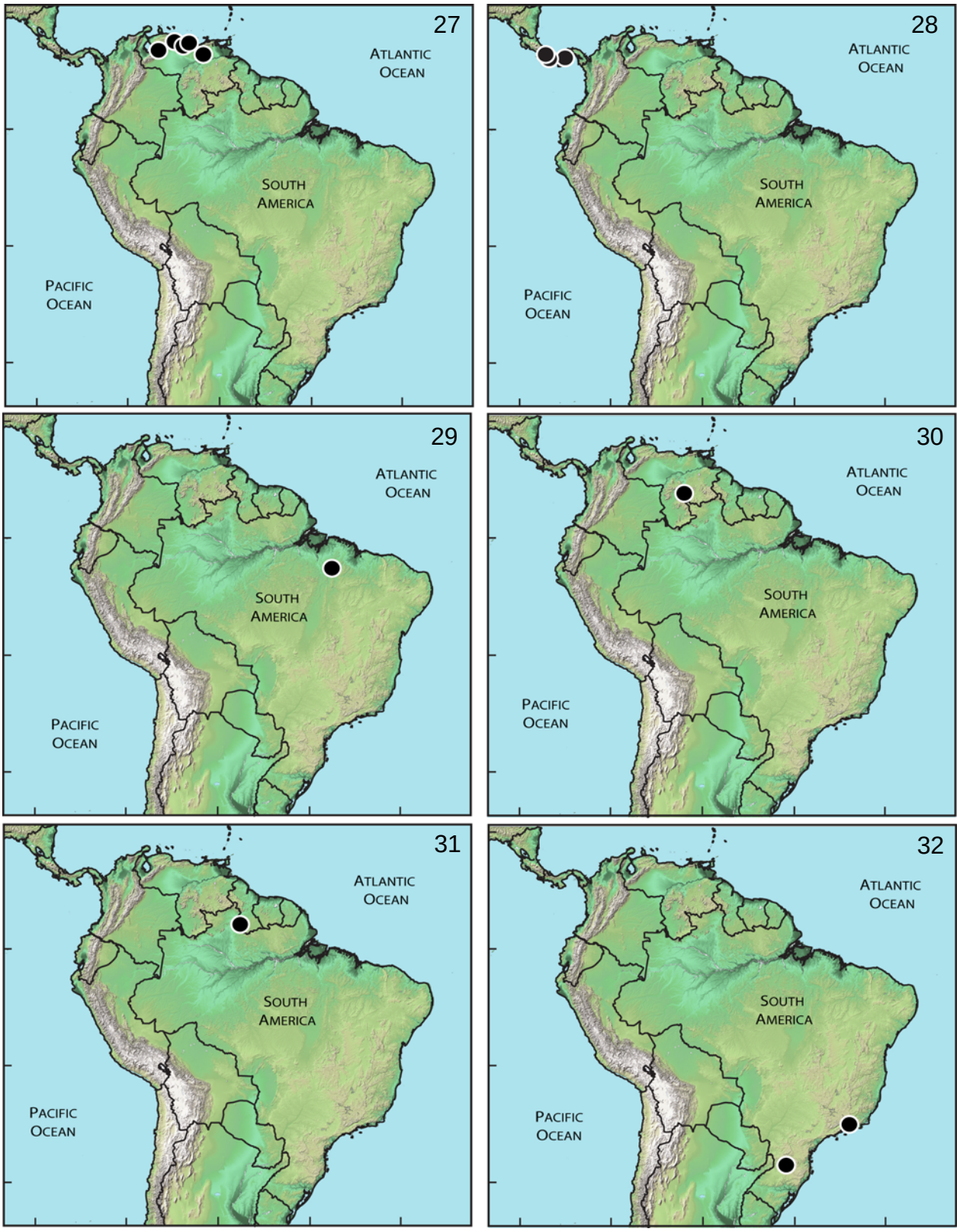
18. Distribution of Lutrochidae genera in the Western Hemisphere. *Auritrochus* spp. (Blue), *Andotrochus* spp. (Green), *Berotrochus* sp. (Orange), *Lutrochus* spp. (Pink), *Saxitrochus* sp. (Yellow).



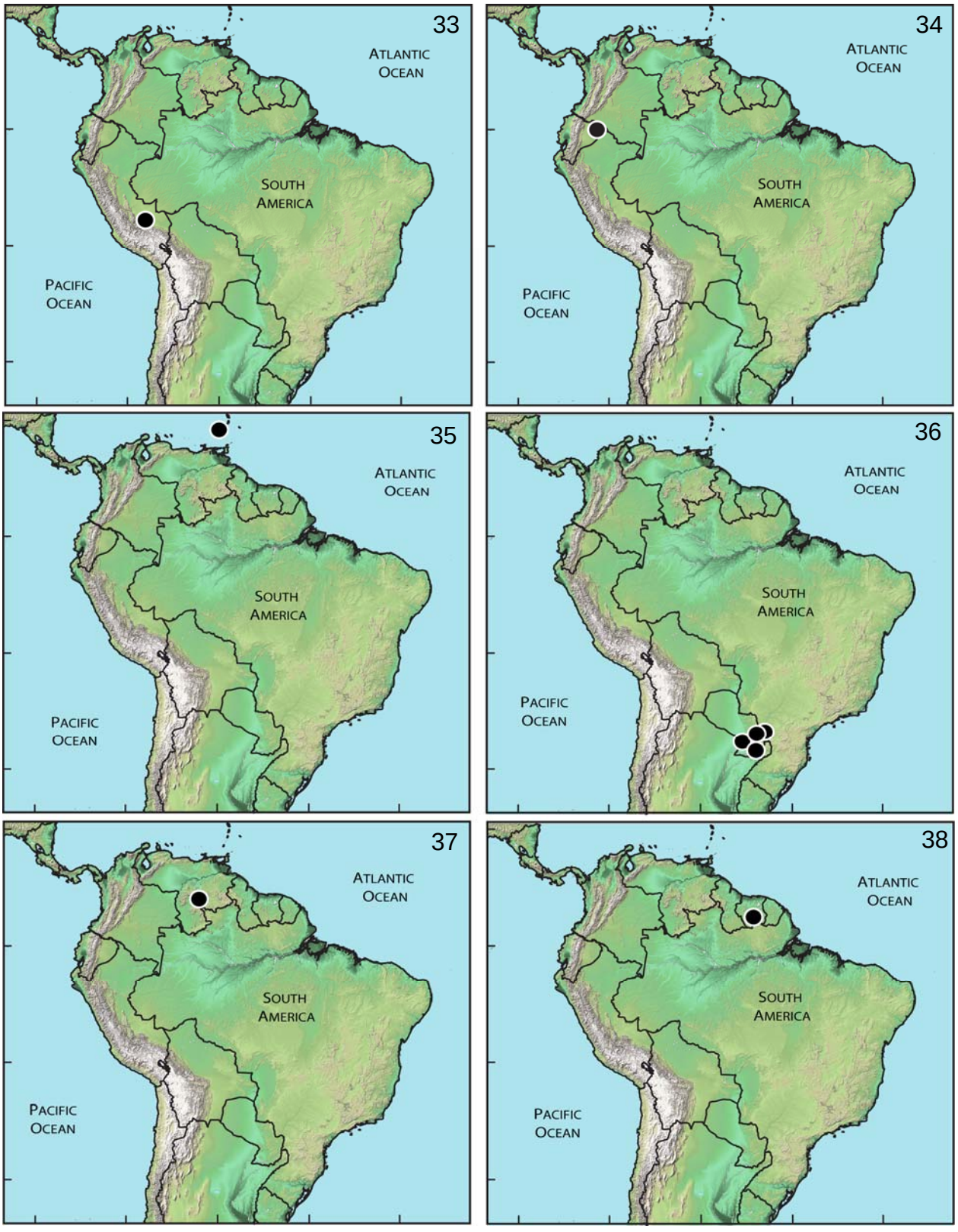
19. Distribution map, *Andotrochus cordobensis*. 20. Distribution map, *A. minutus*.



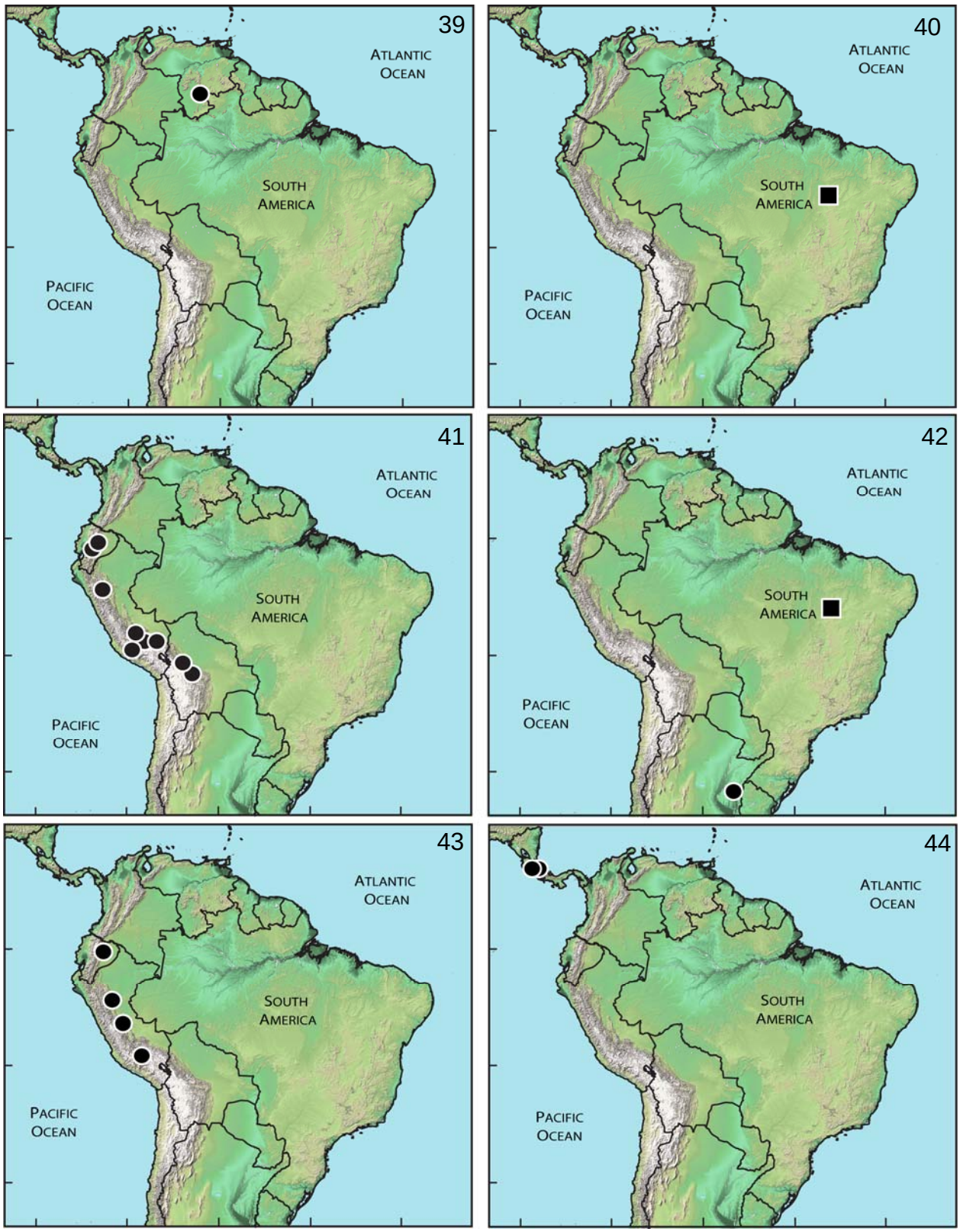
21. Distribution map, *Auritrochus arizonicus*. 22. Distribution map, *A. brunneus*. 23. Distribution map, *A. laticeps*. 24. Distribution map, *A. luteus*. 25 Distribution map, *A. shepardi*. 26. Distribution map, *Berotrochus geniculatus.*



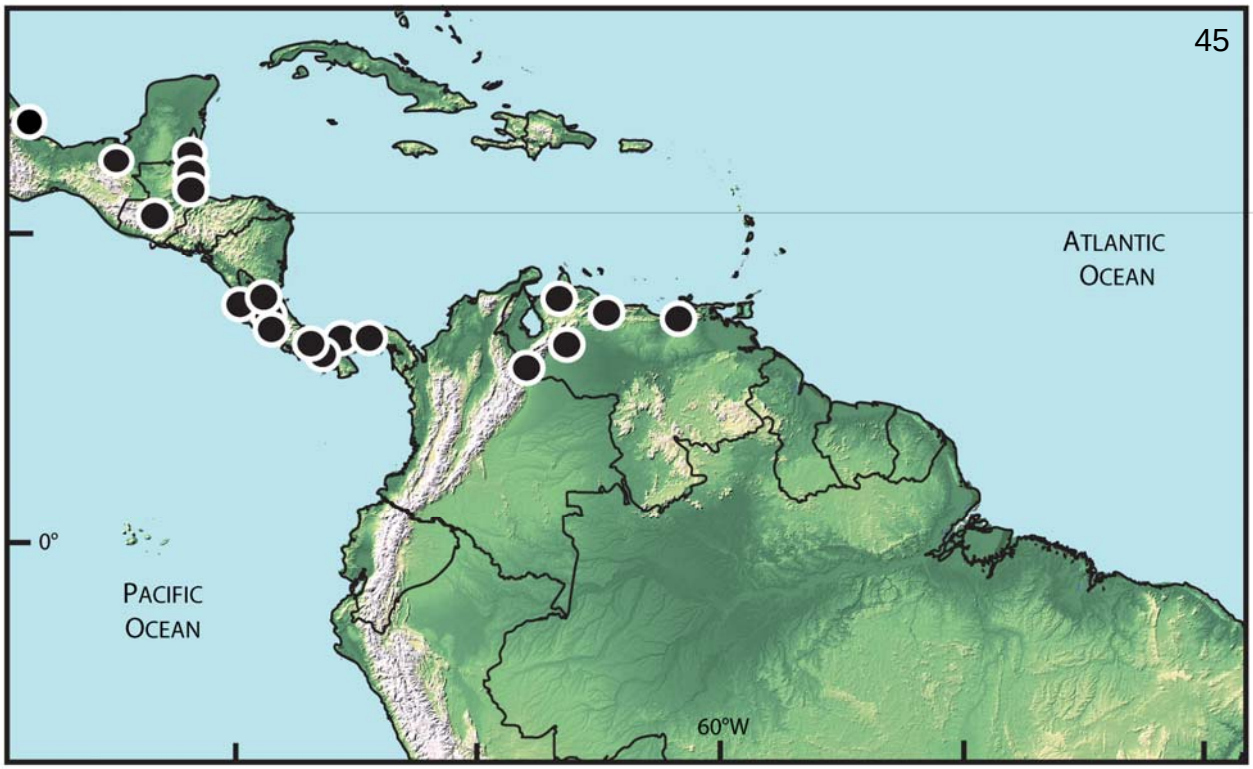
27. Distribution map, *Lutrochus acuminatus*. 28. Distribution map, *L. barrae.* 29. Distribution map, *L. browni*. 30. Distribution map, *L. cauraensis*. 31. Distribution map, *L. funkae*. 32. Distribution map, *L. germari.*

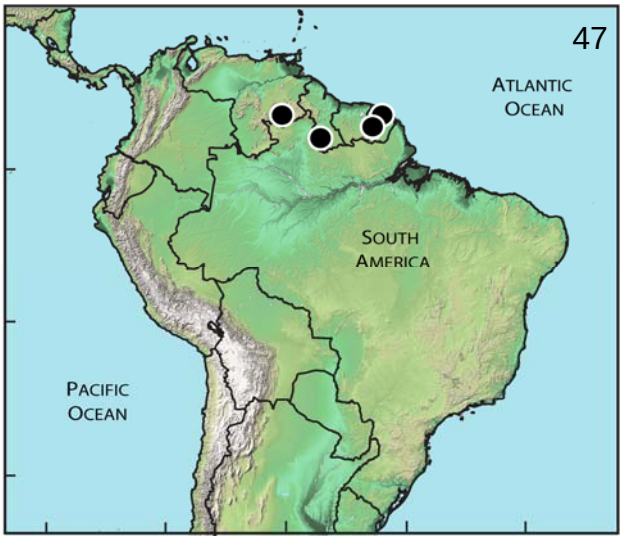


33. Distribution map, *Lutrochus gigas*. 34. Distribution map, *L. gimmeli*. 35. Distribution map, *L. grenadensis*. 36. Distribution map, *L. guarani*. 37. Distribution map, *L. gustafsoni*. 38. Distribution map, *L. leeanneae*.

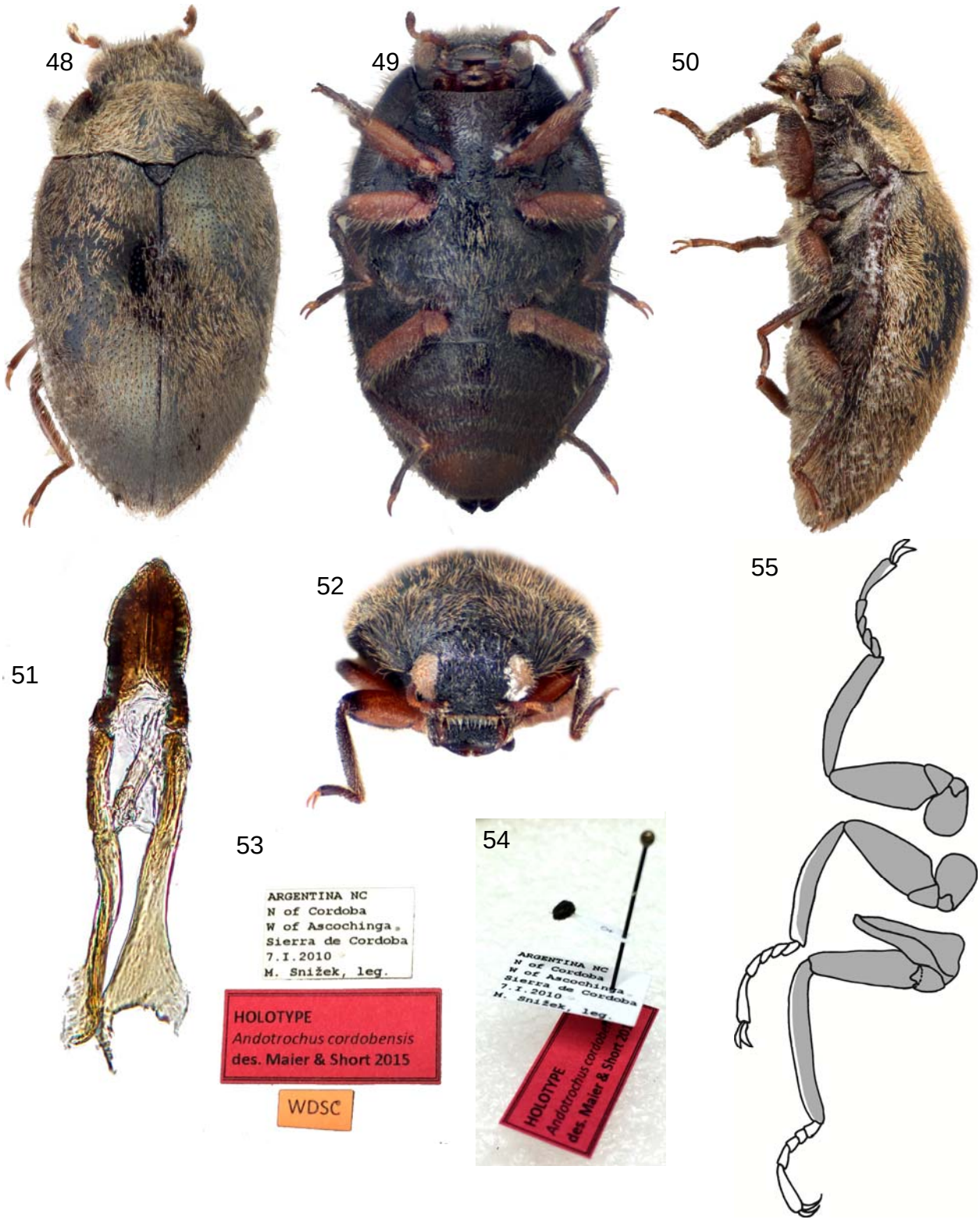


39. Distribution map, *Lutrochus maldonadoi*. 40. Distribution map, *L. misellus (*from "Brazil"). 41. Distribution map, *L. montanus*. 42. Distribution map, *L. pilula* (from "Brazil"). 43. Distribution map, *L. tocache*. 44. Distribution map, *L. torrens.*



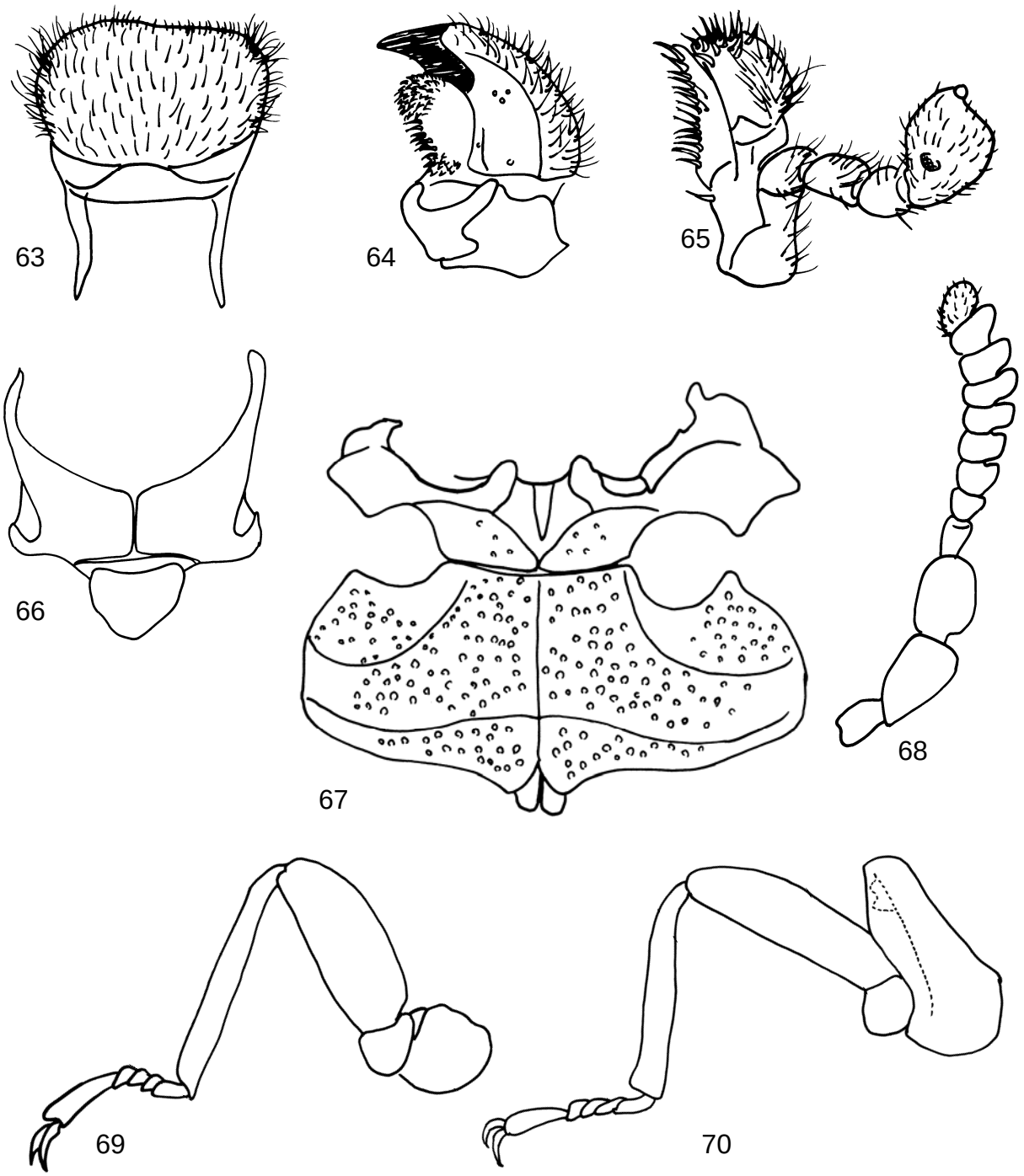


45. Distribution map, *Lutrochus vestitus*-group (including Central and South America). 46. Distribution map, *L. violaceus*. 47. Distribution map, *L. wao*.

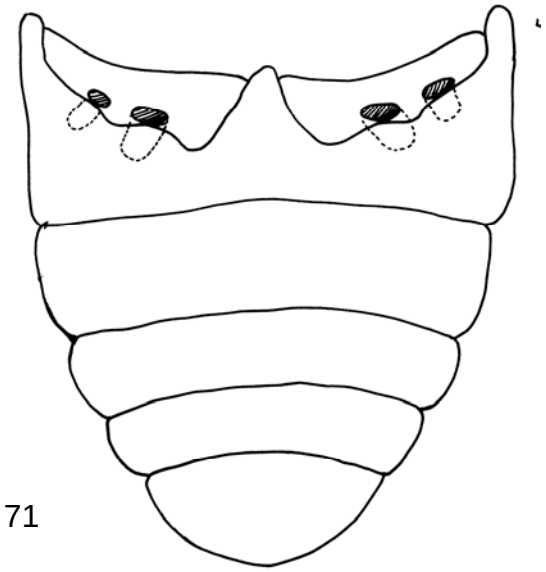


Andotrochus cordobensis Maier & Short 48. Dorsal habitus. 49. Ventral habitus. 50. Lateral habitus. 51. Ovipositor, female. 52. Head, anterior view 53. Holotype, labels. 54. Holotype, posterior oblique view. 55. Legs, schematic representation, showing setation pattern.

Andotrochus minutus (Maier & Short 2013) 56. Dorsal habitus. 57. Ventral habitus. 58. Lateral habitus. 59. Elytral punctation. 60. Scutellum. 61. Hind wings, left and right. 62. Head, oblique view.



Andotrochus minutus (Maier & Short 2013) 63. Mouthparts, labrum. 64. Mouthparts, mandible. 65. Mouthparts, maxilla. 68. Antenna, showing representative setation on apical antennomere. 66. *S*cutellum, cleared. 67. Mesoventrite and metaventrite, cleared. 69. Mesoleg. 70. Metaleg.



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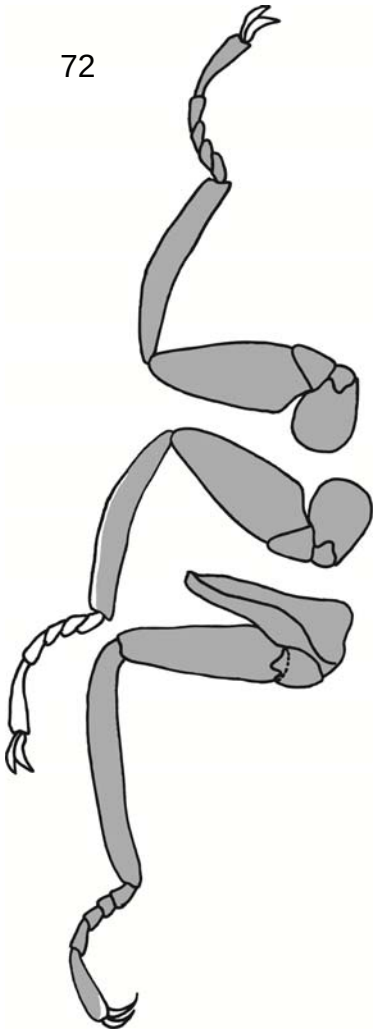

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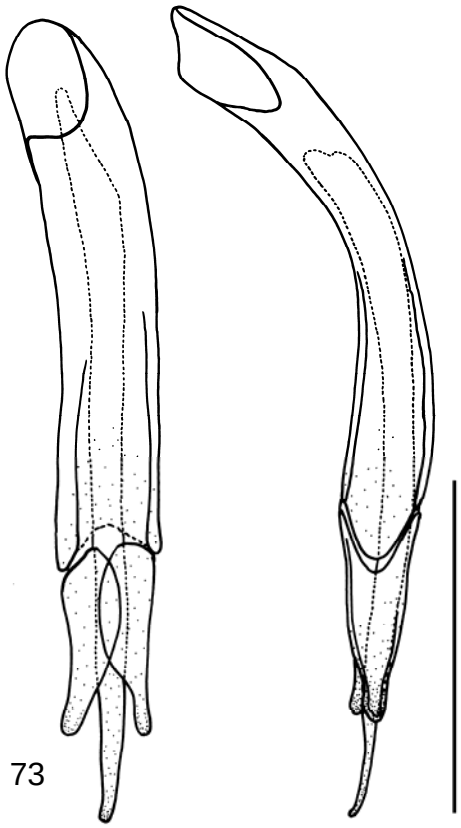

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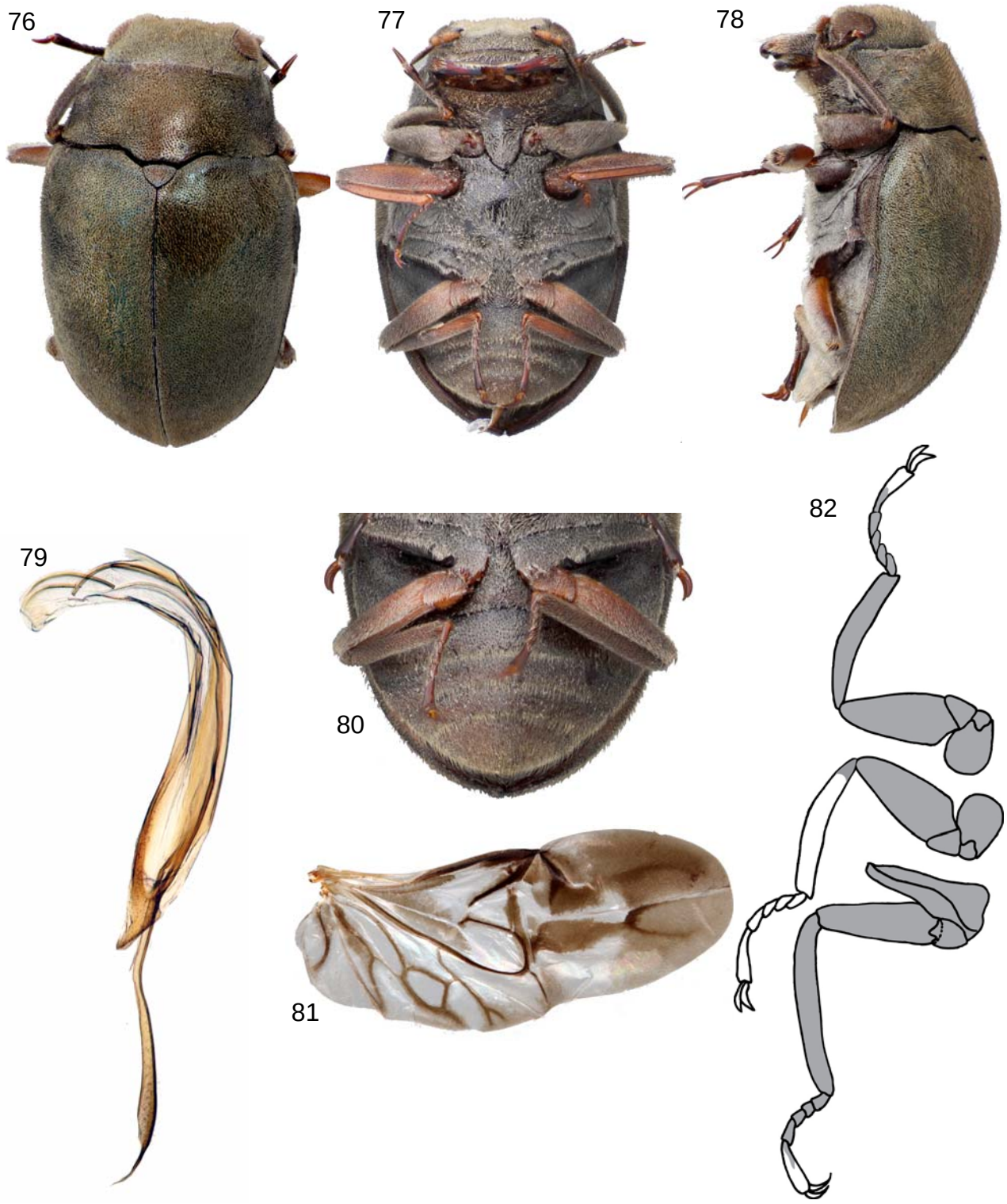
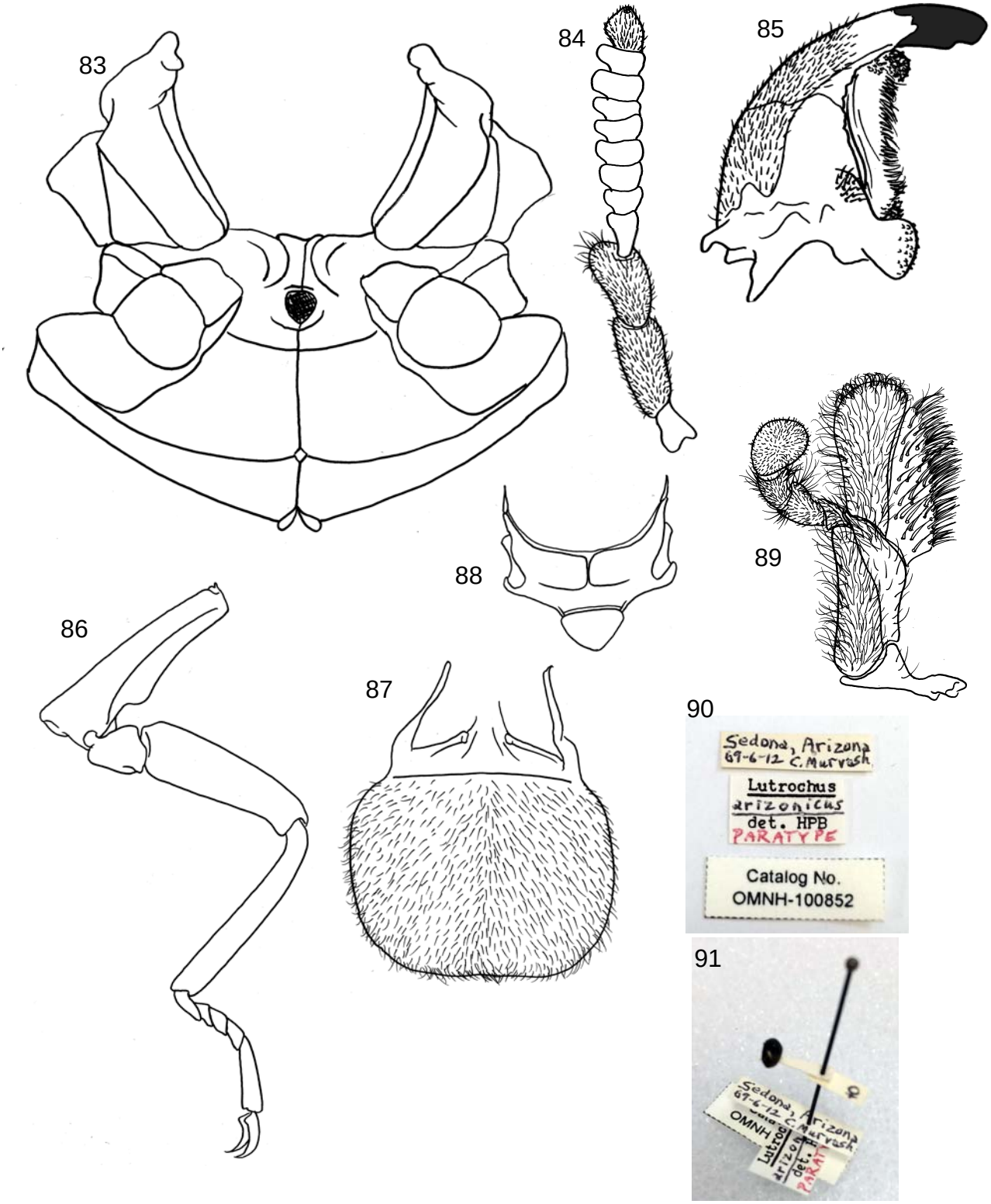
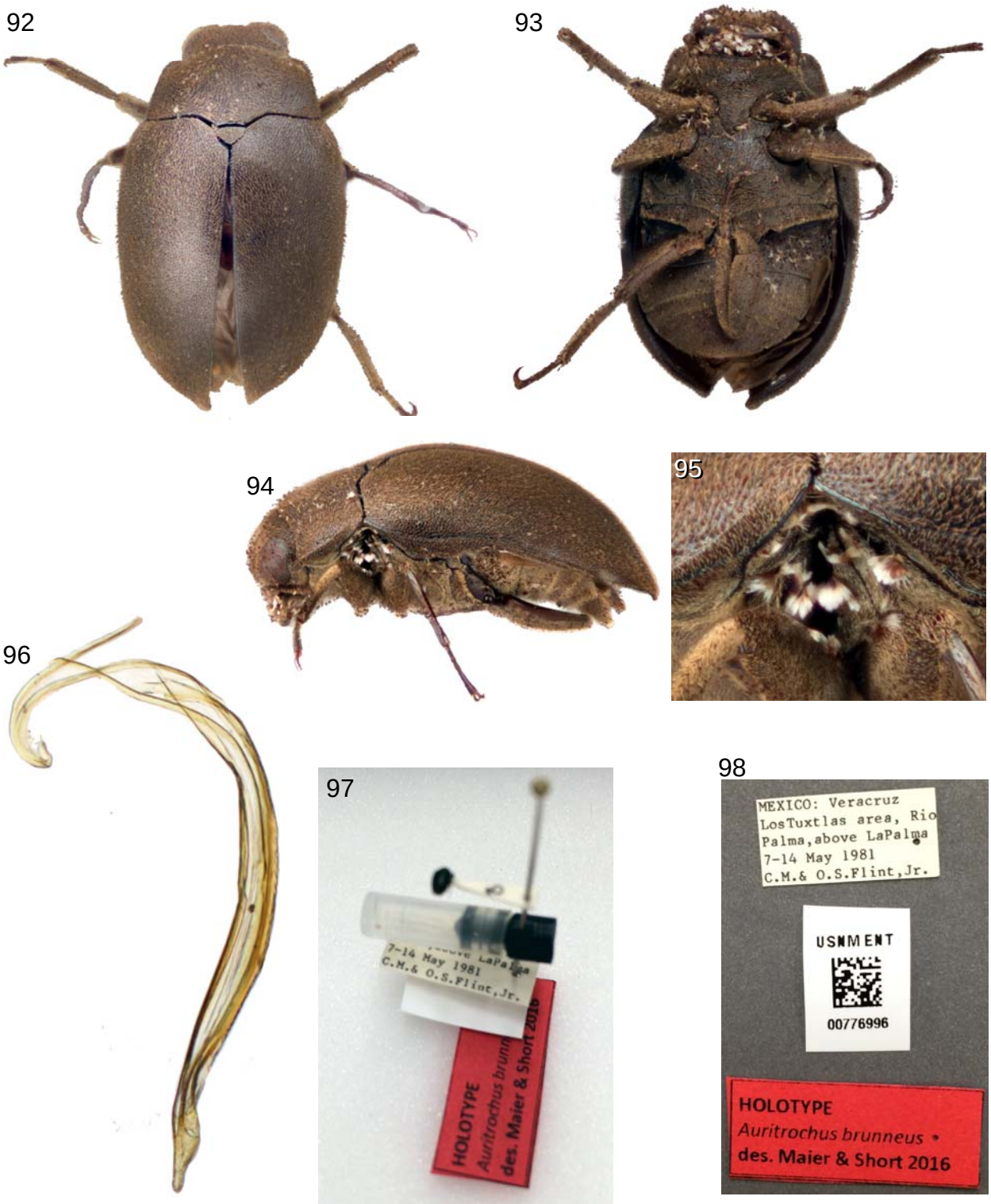
Andotrochus minutus (Maier & Short 2013) 71. Abdomen, male ventral view. 72. Schematic representation of setation patterns on legs. 73. Male genitalia, dorsal/lateral view. 74. Holotype specimen, oblique view. 75. Holotype specimen, dorsal view. 76. Holotype specimen, labels.



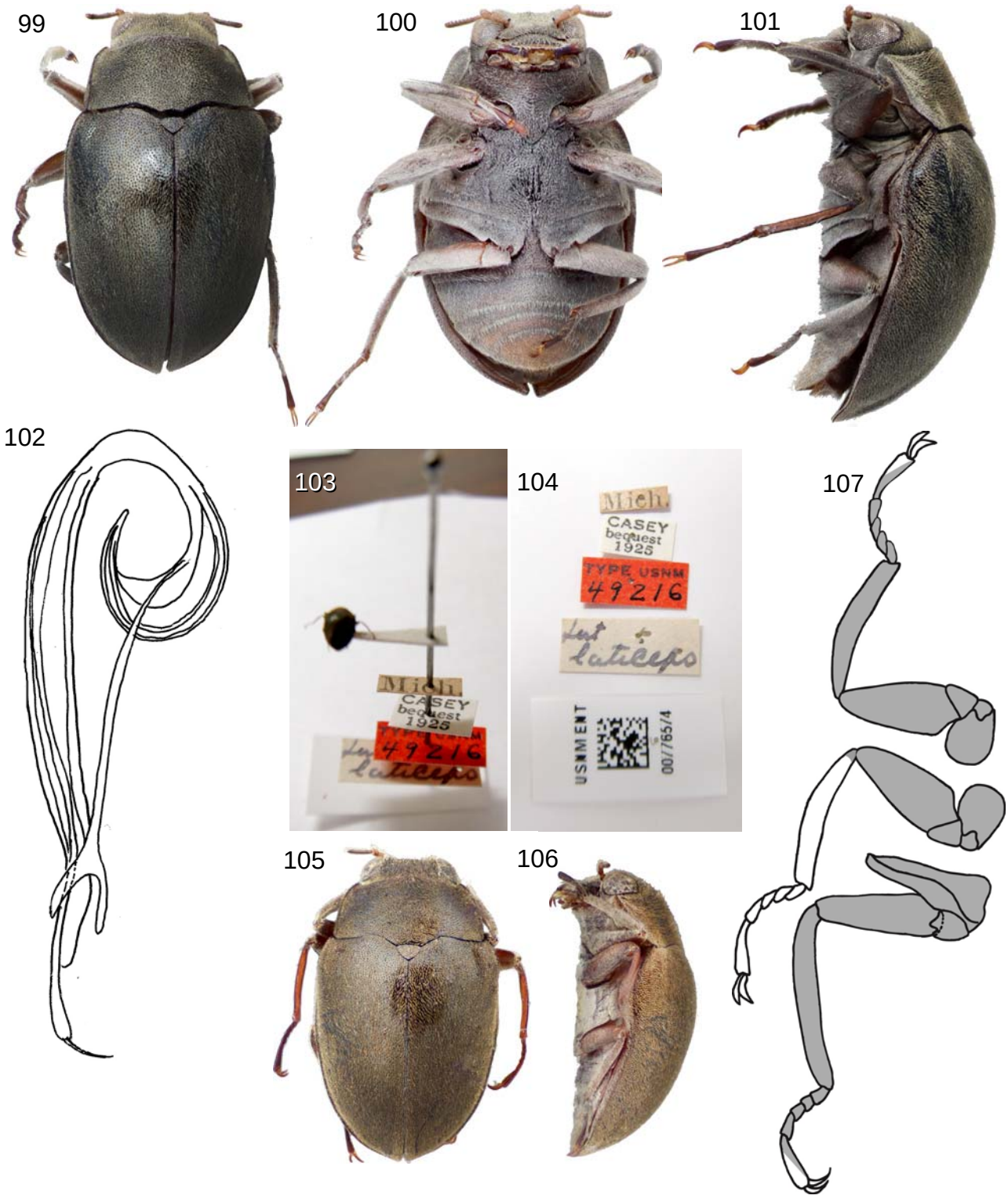
Auritrochus arizonicus (Brown & Murvosh) 76. Dorsal habitus. 77. Ventral habitus. 78. Lateral Habitus. 79. Aedeagus, dorsal/lateral views. 80. Abdomen, female, ventral view. 81. Wing. 82. Legs, schematic view, showing setation.



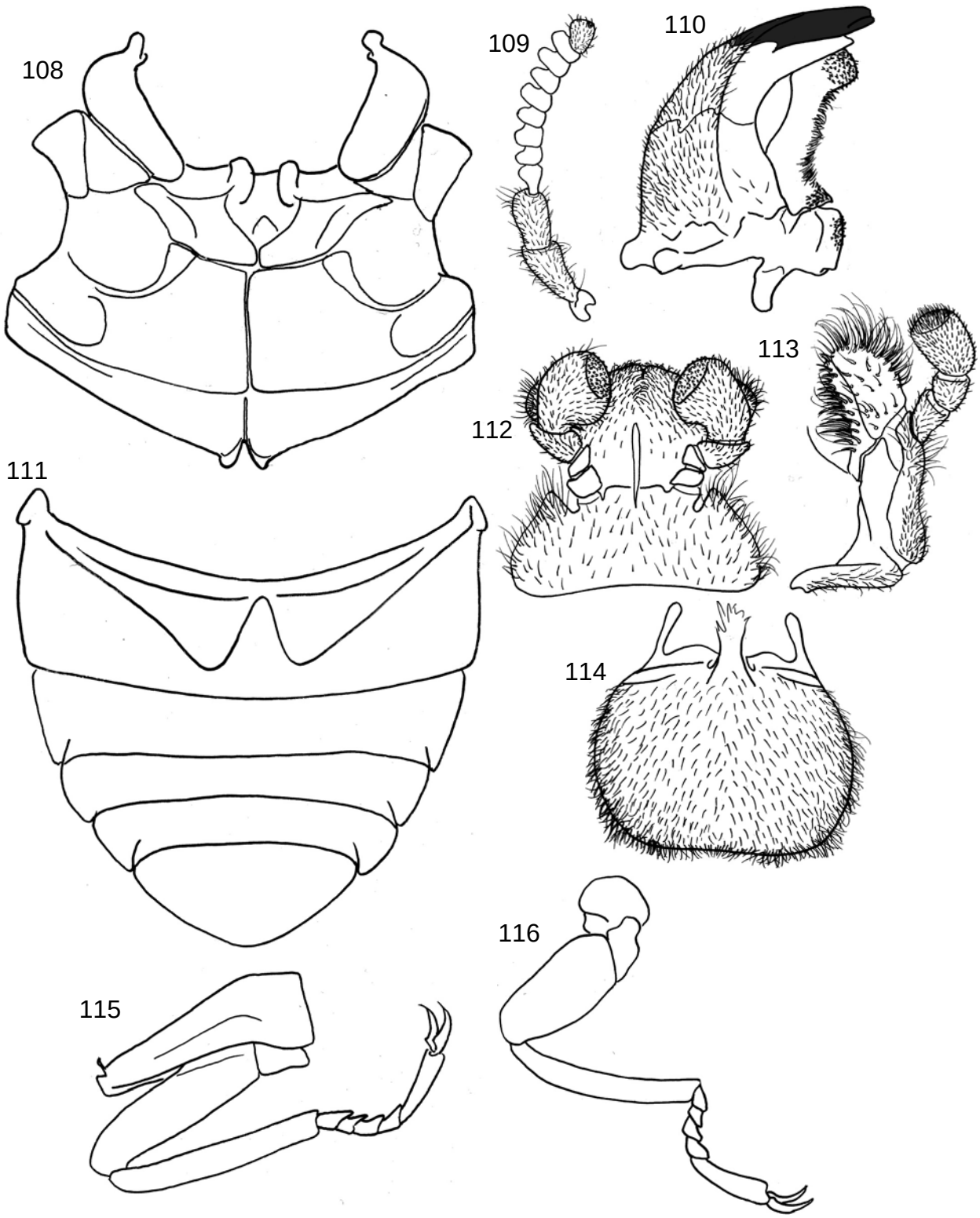
Auritrochus arizonicus (Brown & Murvosh) 83. Meso- and Meta-ventrites, cleared. 84. Antenna, showing representative setation on first and last antennomeres. 85. Lateral Mandible. 86. Metaleg. 87. Labrum. 88. Scutellum. 89. Maxilla. 90. Paratype labels. 91. Paratype, oblique view.



Auritrochus brunneus n. sp. 92. Dorsal habitus. 93. Ventral habitus. 94. Lateral Habitus. 95. Close-up of lateral view of paratype, showing Laboulbeniales fruiting bodies. 96. Aedeagus, lateral view. 97. Holotype, posterior view. 98. Holotype labels.



Auritrochus laticeps (Casey) 99. Dorsal habitus. 100. Ventral habitus. 101. Lateral Habitus. 102. Aedeagus, lateral view. 103. Lectotype specimen, posterior view. 104. Lectotype labels. 105. Lectotype specimen, dorsal view. 106. Lectotype specimen, lateral view. 107. Legs, schematic view, showing setation.



Auritrochus laticeps (Casey) 108. Meso- and Meta-ventrites, cleared. 109. Antenna, showing representative setation on first and last antennomeres. 110. Mandible. 112. Labium. 113. Maxilla. 114. Labrum. 111. Abdomen, Female. 115. Metaleg. 116. Mesoleg.

Auritrochus laticeps (Casey) 117. Collecting *L. laticeps* at Elk River, Kansas. 118. *L. laticeps in situ* at Elk River, Kansas. 119. Habitat at Elk River Falls, Kansas. 120. Habitat at Spavinaw Creek, Oklahoma.

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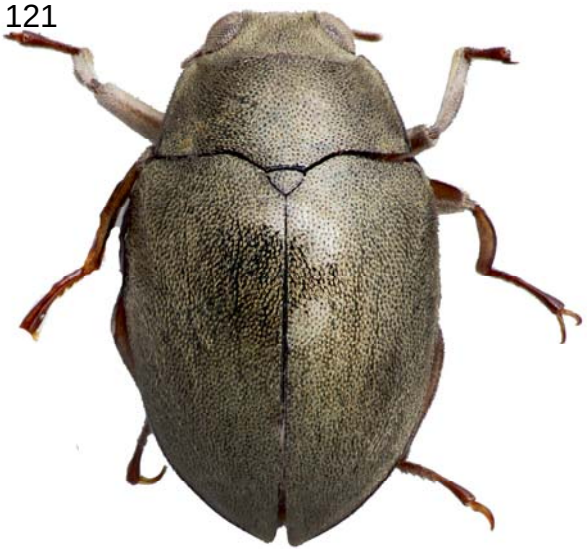

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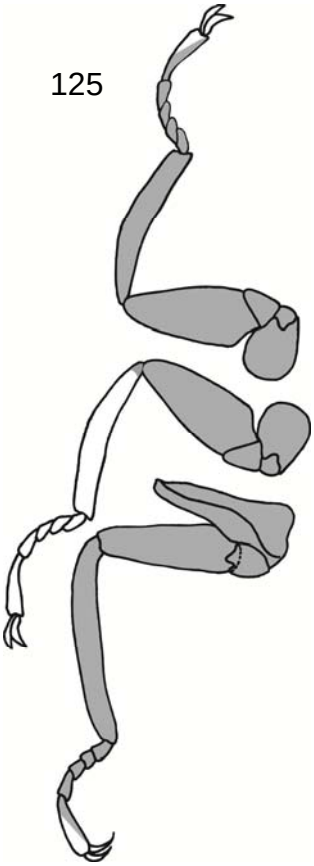
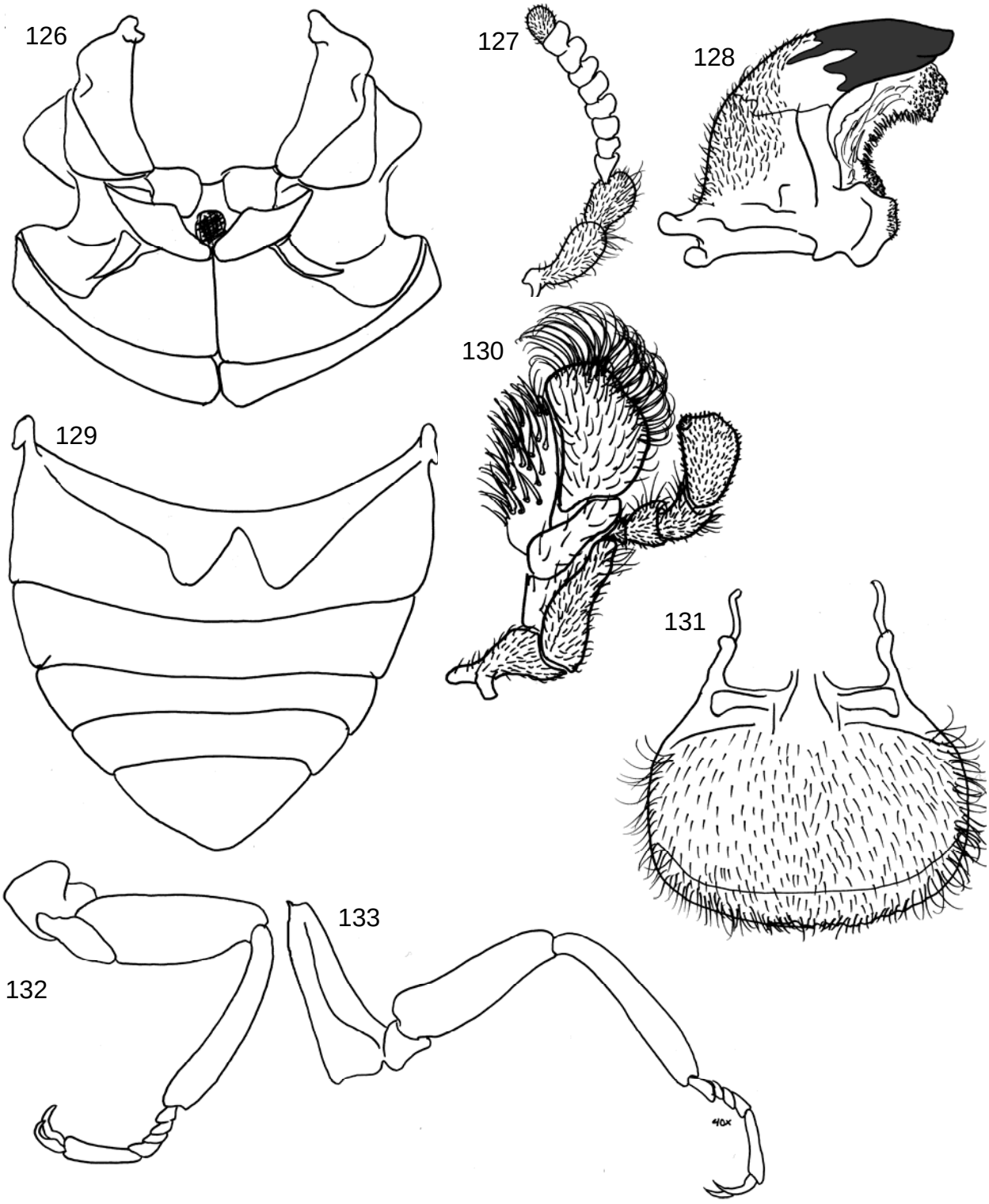
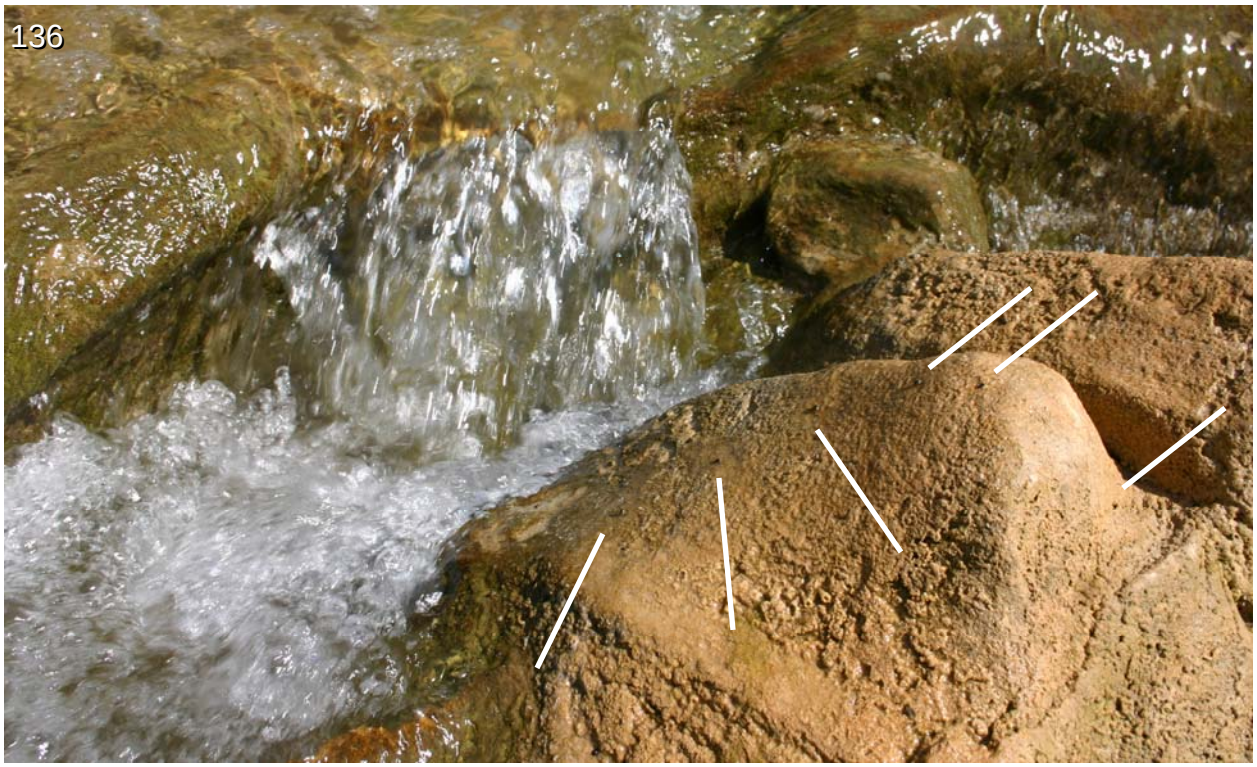


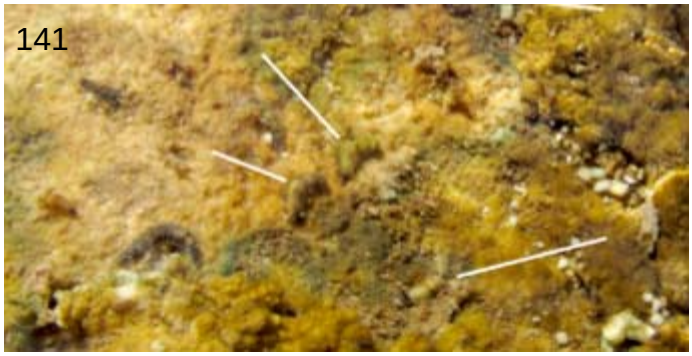
Auritrochus luteus (LeConte) 121. Dorsal habitus. 122. Ventral habitus. 123. Lateral Habitus. 124. Holotype labels. 125. Legs, schematic view, showing setation.



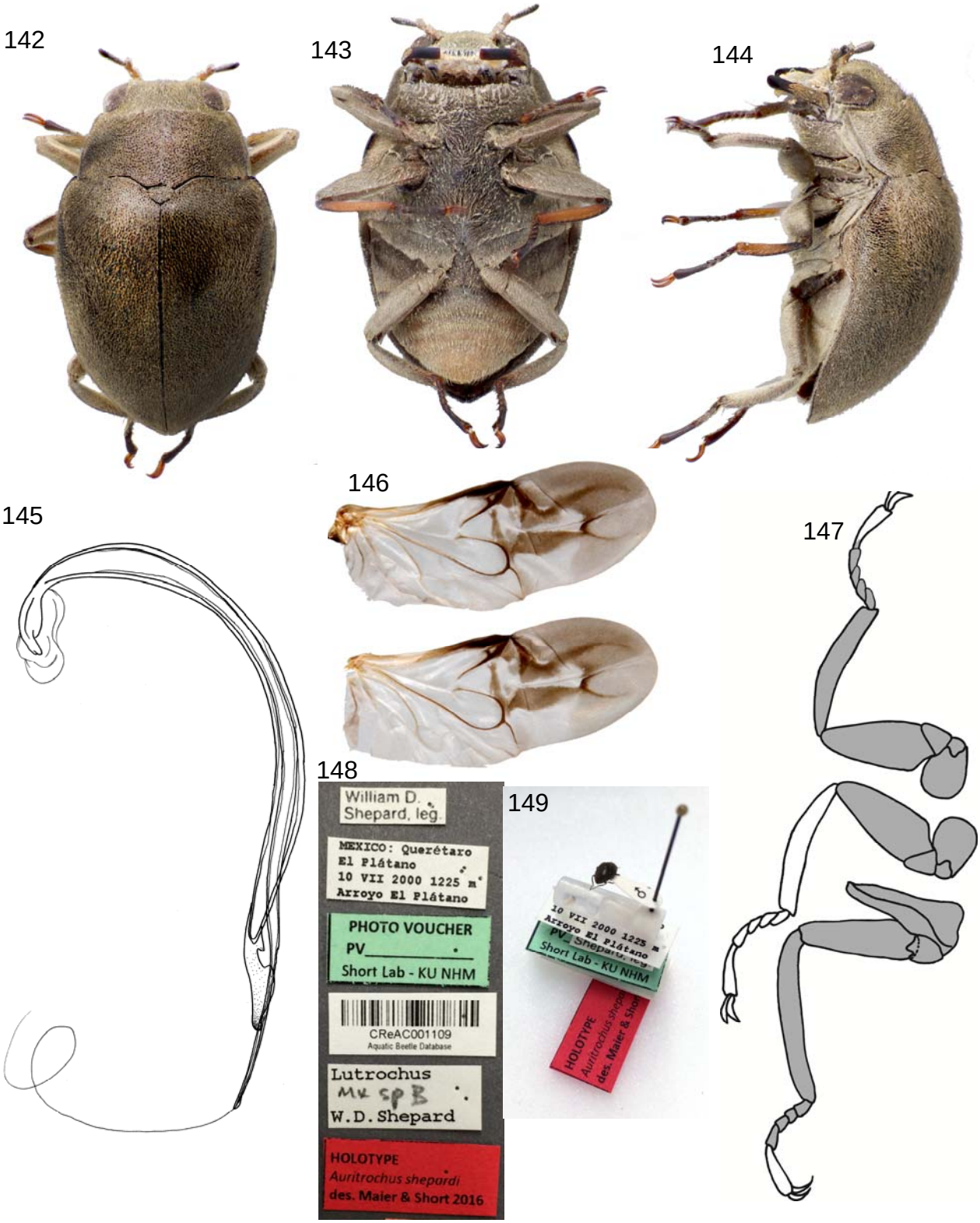
Auritrochus luteus (LeConte) 126. Meso- and Meta-ventrites, cleared. 127. Antenna, showing representative setation on first and last antennomeres. 128. Mandible. 129. Abdomen, Female. 130. Maxilla. 131. Labrum. 132. Mesoleg. 133. Metaleg.



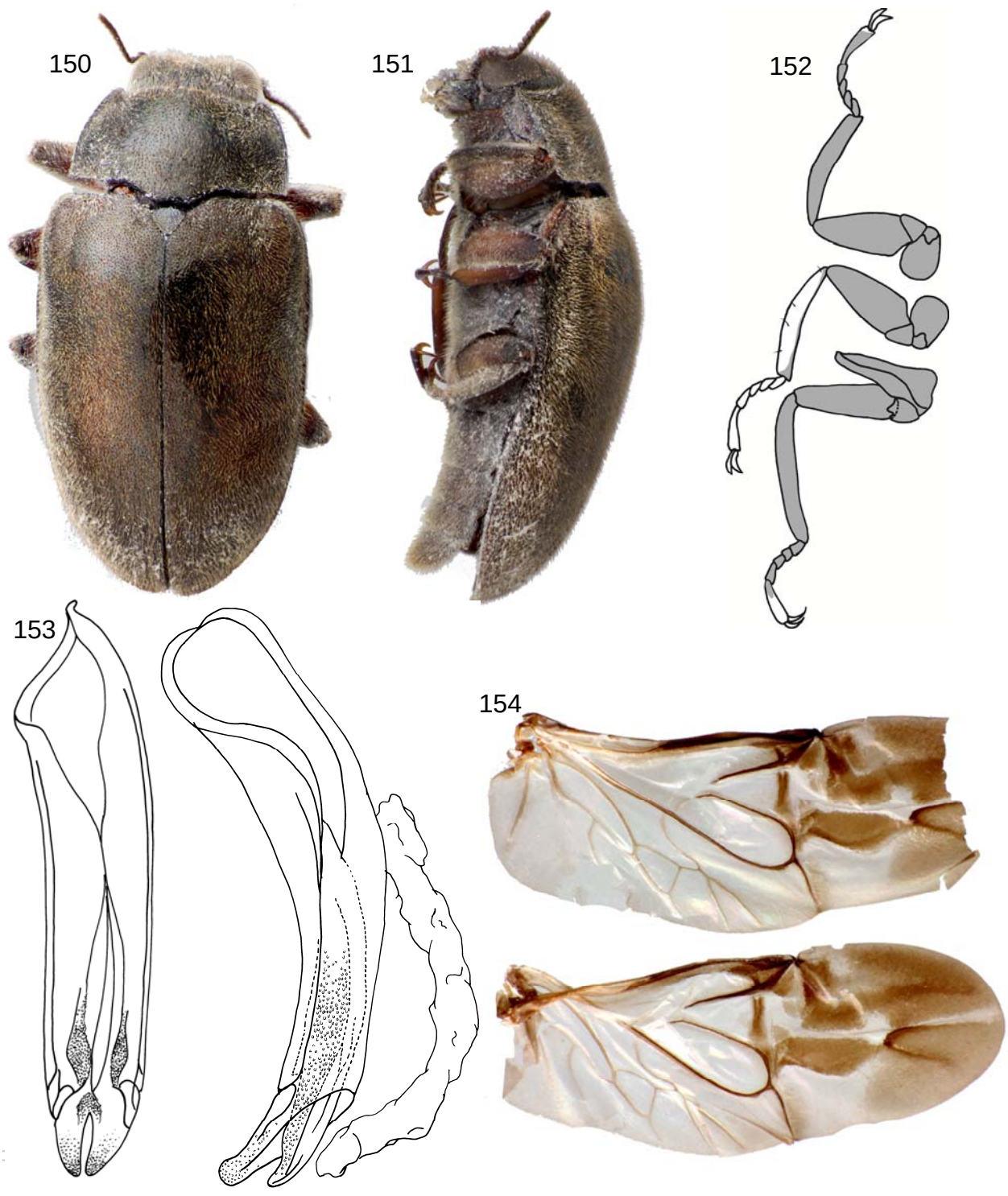
Auritrochus luteus (LeConte) 134. Habitat at Turner Falls, Oklahoma. 135. *A. luteus* mating *in situ* at Turner Falls, Oklahoma. 136. Microhabitat at Turner Falls, Oklahoma, dots on rock in foreground are the travertine beetles, grazing on periphyton.



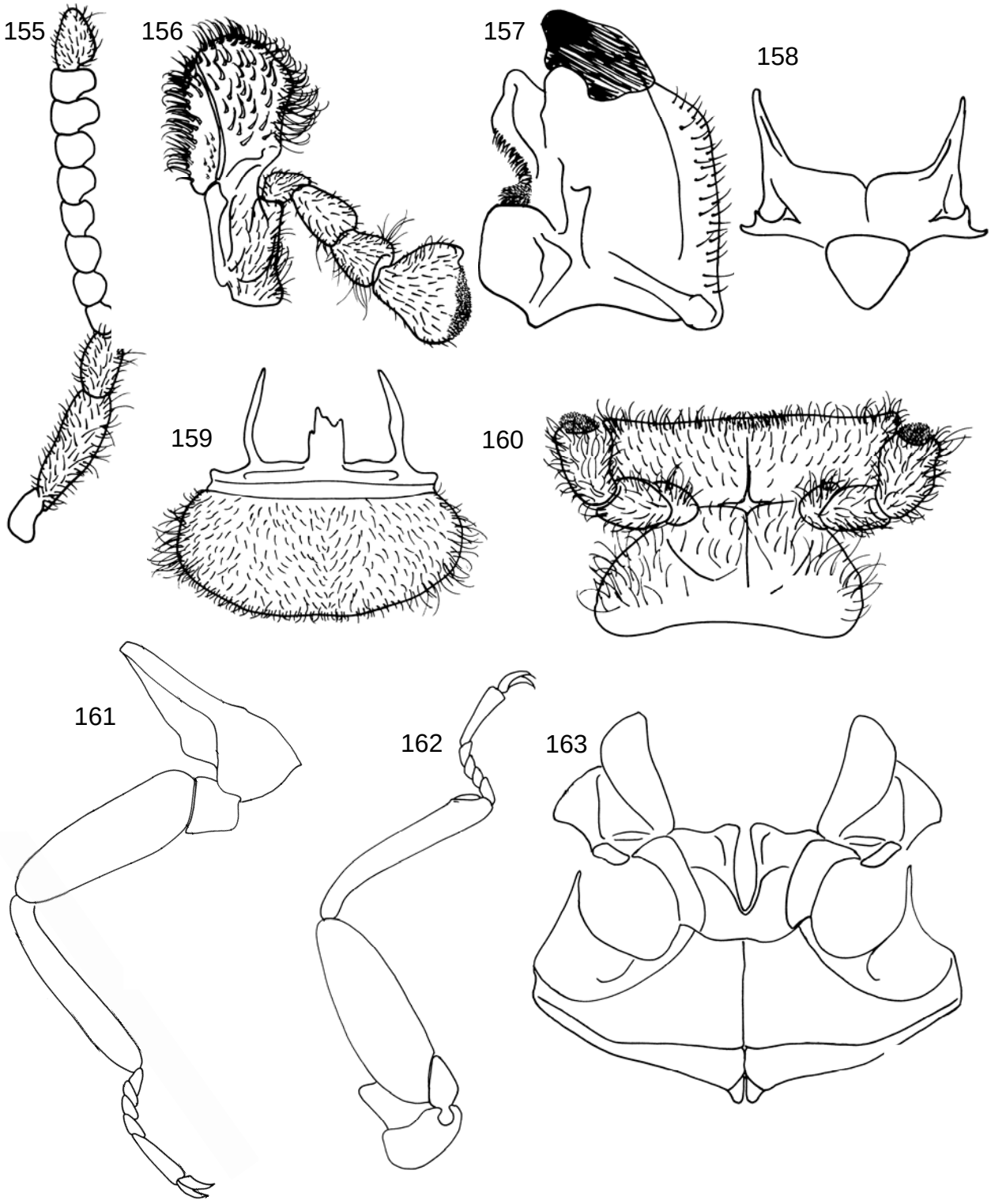
Auritrochus luteus (LeConte) 137. Habitat at Black River, NM. 138. Microhabitat under culvert at Black River, NM. 139. Habitat at tributary to the Black River, NM. 140. Adult beetle *in situ* at Turner Falls, Oklahoma. 141. *A. luteus* larvae *in situ* at Turner Falls, Oklahoma.



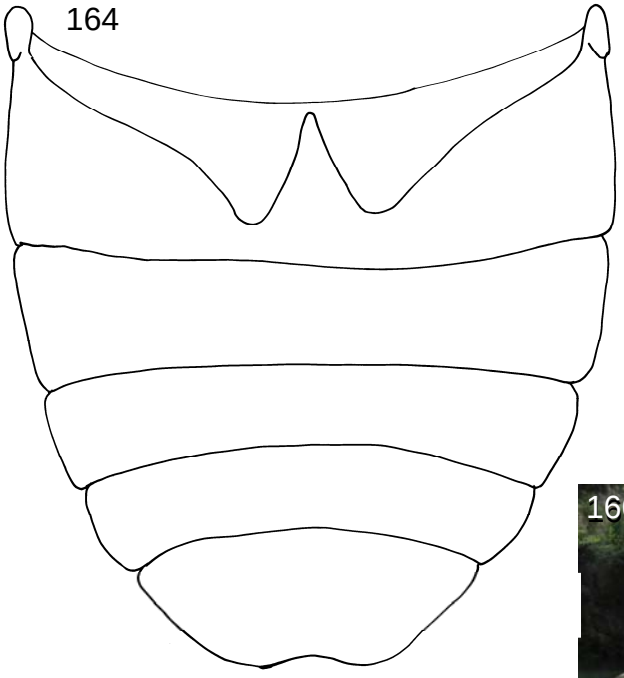
Auritrochus shepardi n. sp. 142. Dorsal habitus. 143. Ventral habitus. 144. Lateral Habitus. 145. Aedeagus, lateral view. 146. Wings, slide mounted. 147. Schematic diagram of legs, showing setation pattern. 148. Holotype labels. 149. Holotype, posterior view.



Berotrochus geniculatus (Chevolat, 1894) 150. Dorsal habitus. 151. Lateral habitus. 152. Setation of legs. 153. Male genitalia, dorsal/lateral views. 154. Hind wings, left and right (Note: wing was torn during dissection)



Berotrochus geniculatus (Chevolat, 1894) 155. Antenna, showing representative setation on apical antennomere. 156. Mouthparts, maxilla. 157. Mouthparts, mandible. 158. Scutellum, cleared. 159. Mouthparts, labrum. 160. Mouthparts, labium. 161. Metaleg. 162. Mesoleg. 163. Mesoventrite and metaventrite, cleared.



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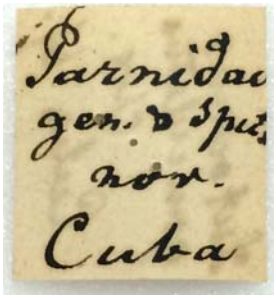
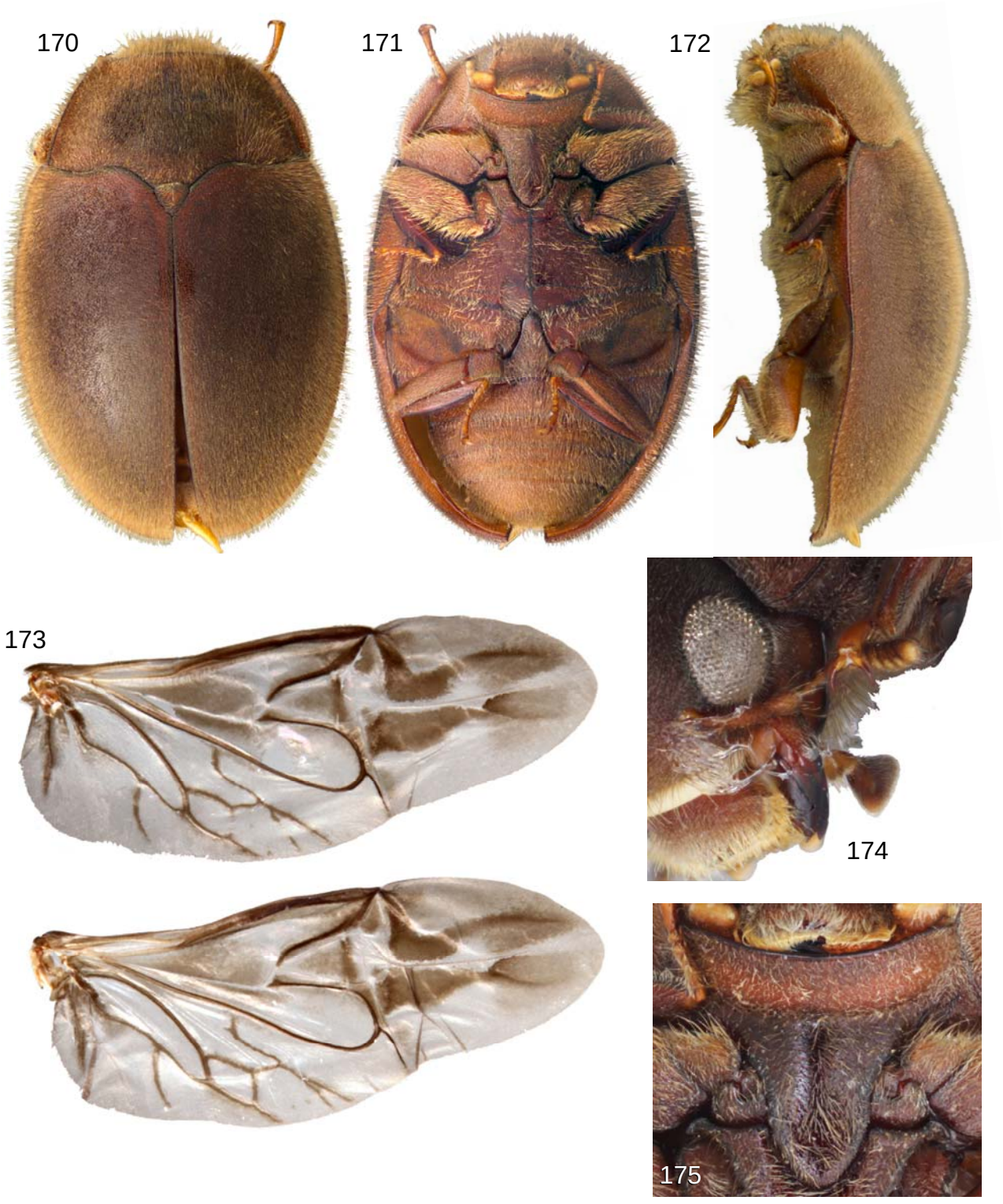
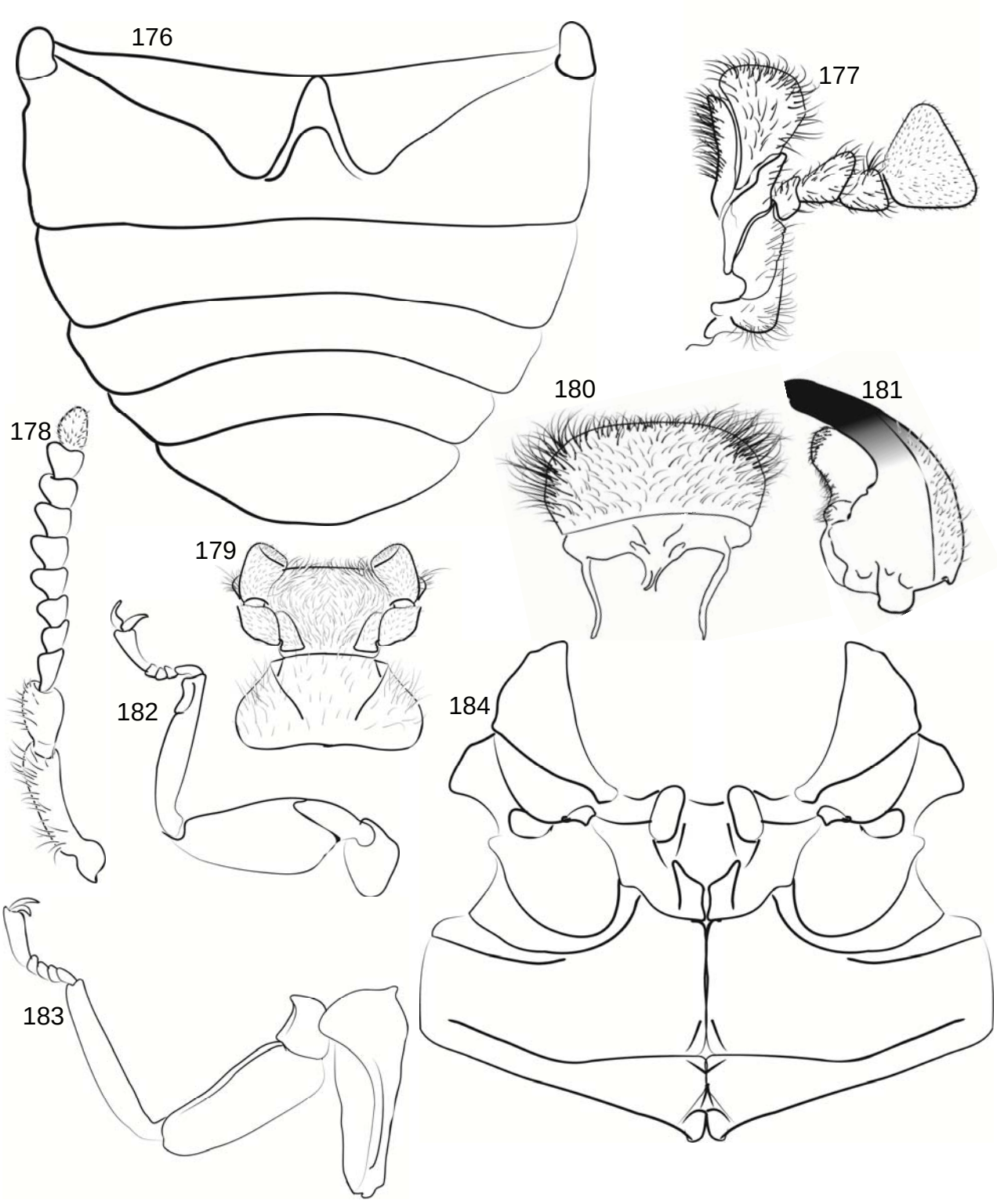


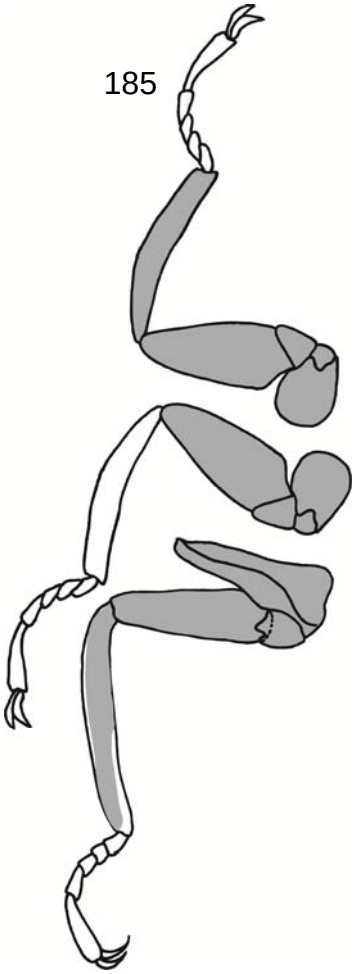
Berotrochus geniculatus (Chevolat, 1894) 164. Abdomen, male ventral view. 165. Habitat of *N. geniculatus* at Riverie Glace, Haiti (photo: Debbie Baker). 166. Habitat of *N. geniculatus* at Riverie Glace, Haiti, alternate view (photo: Debbie Baker). 167. Labels of Lectotype specimen, indicating examination by Chevrolat. 168. Labels of Syntype series, indicating new species. 169. Lectotype specimen and paralectotype specimens, oblique view.

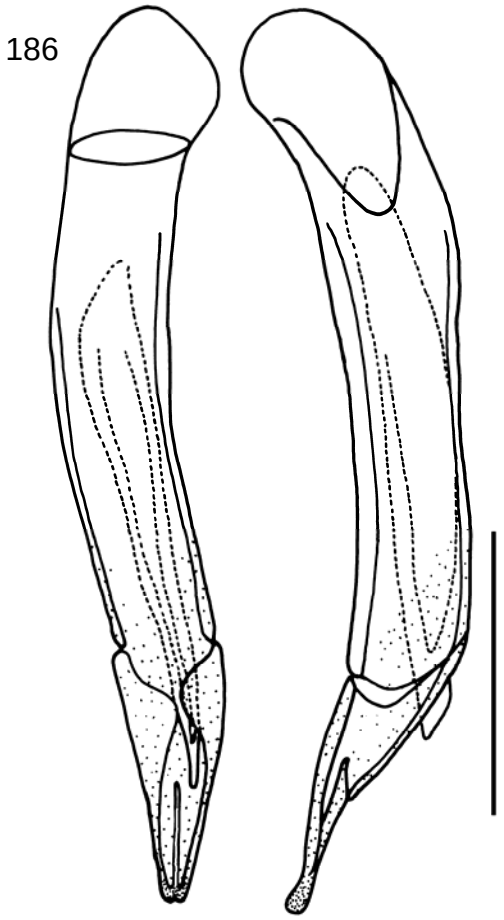


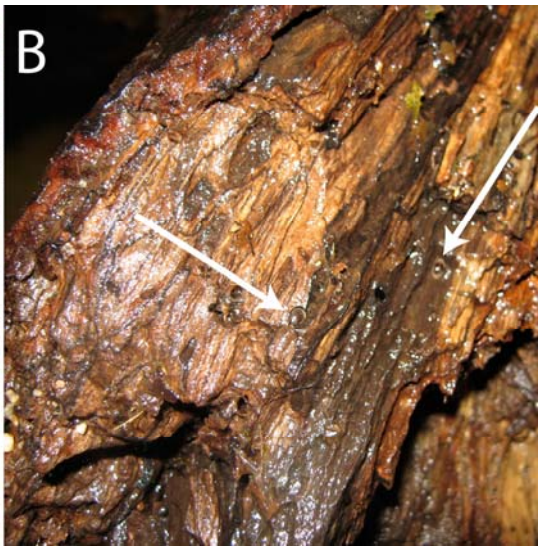
Lutrochus acuminatus Grouvelle, 1893 170. Dorsal habitus. 171. Ventral habitus. 172. Lateral Habitus. 173. Wings, left and right. 174. Head, oblique view, showing maxillary palps. 175. Prosternum, showing transverse fold.



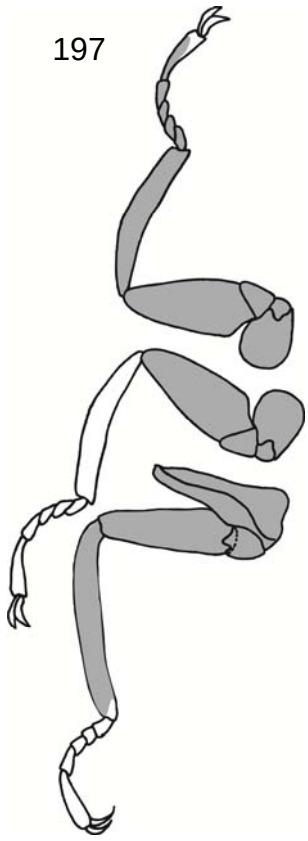
Lutrochus acuminatus Grouvelle, 1893 176. Abdomen, male, ventral view. 177. Mouthparts, Maxilla. 178. Antenna, showing representative setation on distal antennomere. 179. Mouthparts, Labium. 180. Mouthparts, Labrum. 181. Mouthparts, Mandible. 182. Mesoleg. 183. Metaleg. 184. Meso– and metaventrites.



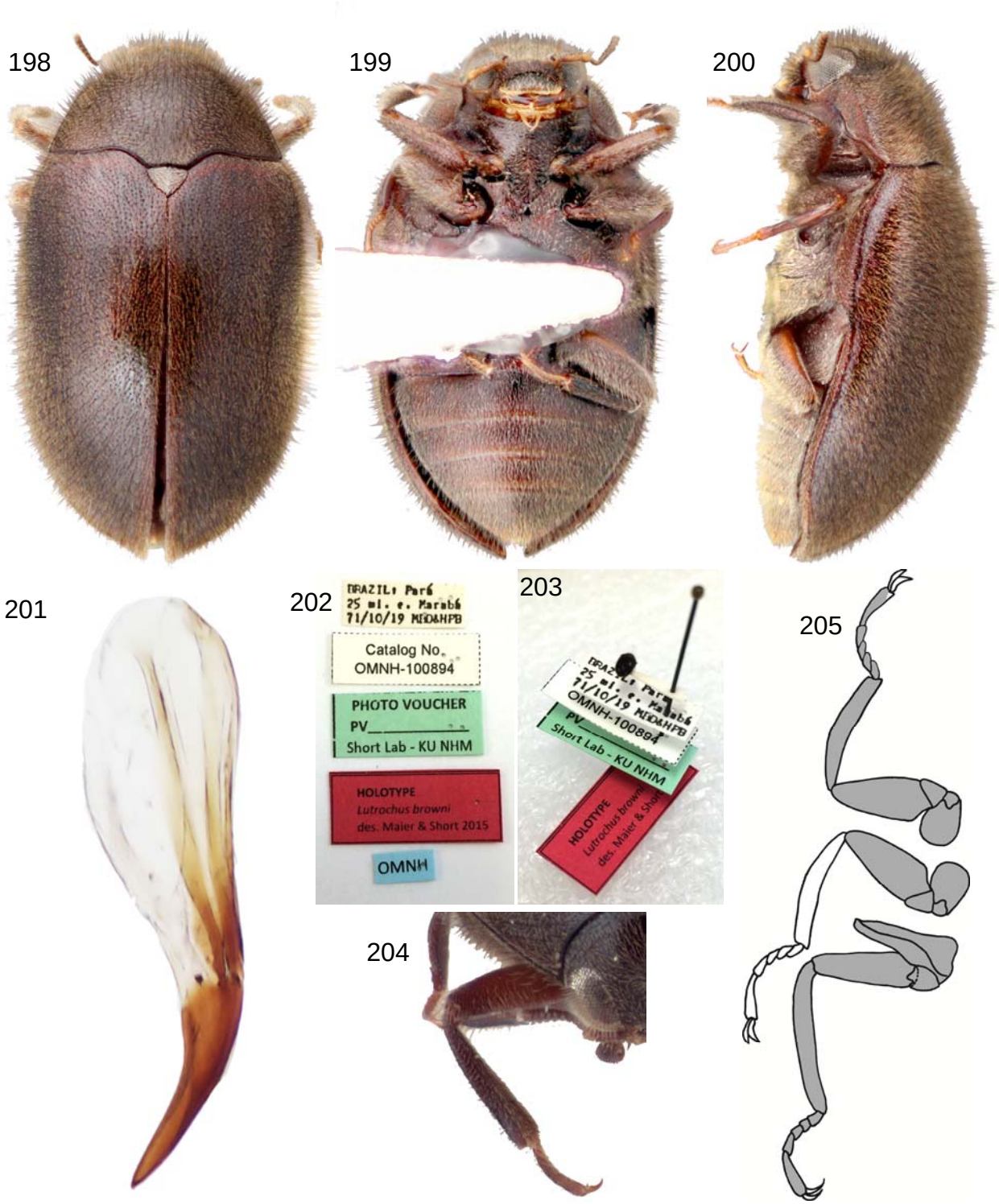




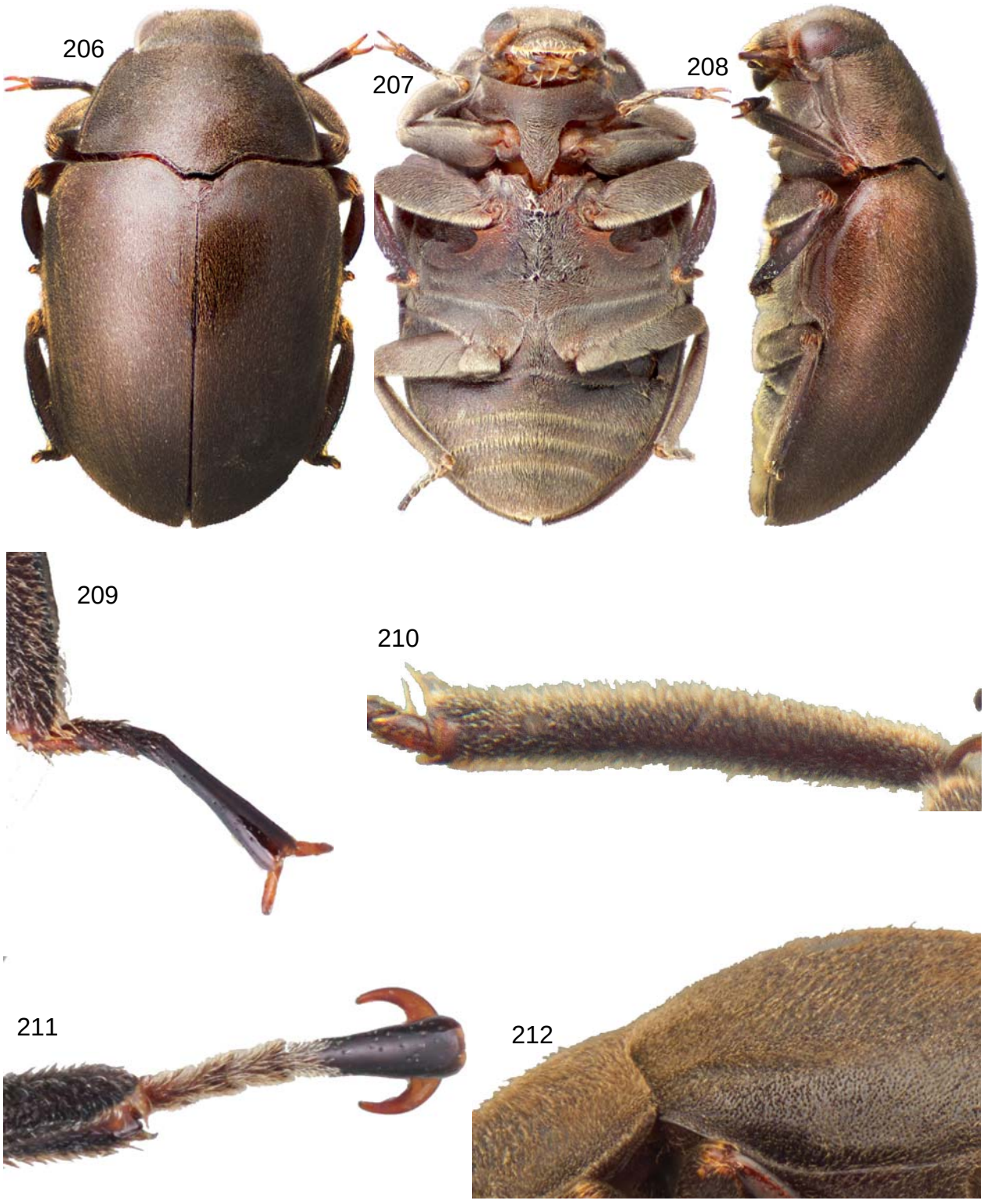
Lutrochus acuminatus Grouvelle, 1893 185. Schematic representation of setation of legs. 186. Male genitalia, dorsal and lateral views. 187. Holotype specimen, oblique view. 188. Holotype specimen labels. 189. Habitat, Merida, Venezuela.



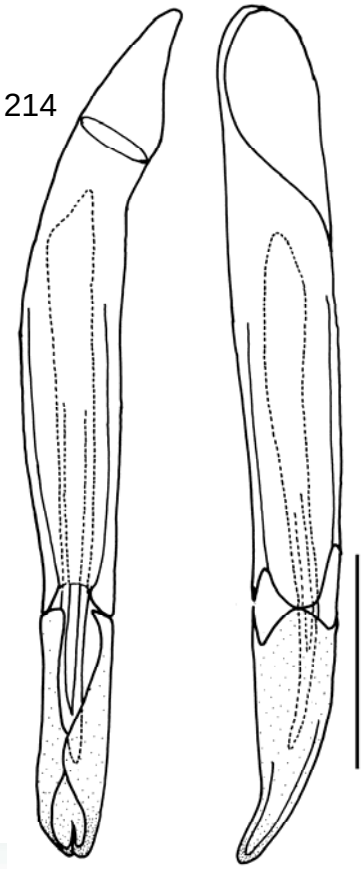
Lutrochus barrae Maier & Short 190. Dorsal habitus. 191. Ventral habitus. 192. Lateral Habitus. 193. Aedeagus, Dorsal/Lateral Views. 194. Holotype specimen labels. 195. Holotype specimen, posterior view. 196. Protarsus, showing setation. 197. Schematic representation of setation of legs.

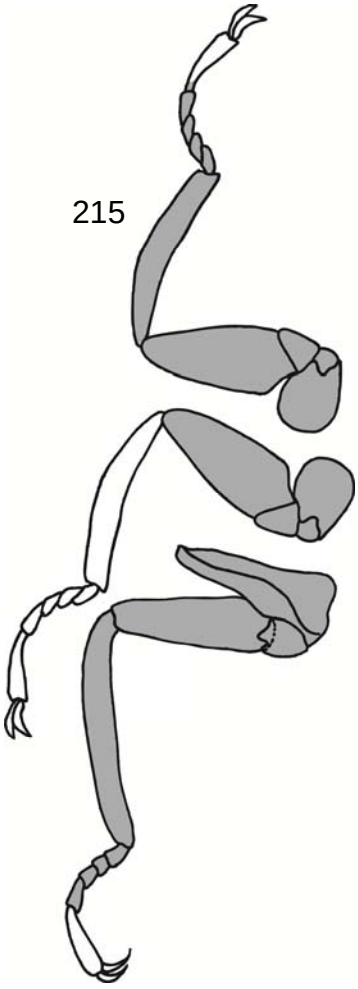


Lutrochus browni **n. sp.** 198. Dorsal habitus. 199. Ventral habitus. 200. Lateral habitus. 201. Ovipositor. 202. Holotype specimen labels. 203. Holotype specimen, posterior view. 204. Oblique view, showing antenna, apical maxillary palpomere and pro-leg. 205. Schematic representation of setation of legs.

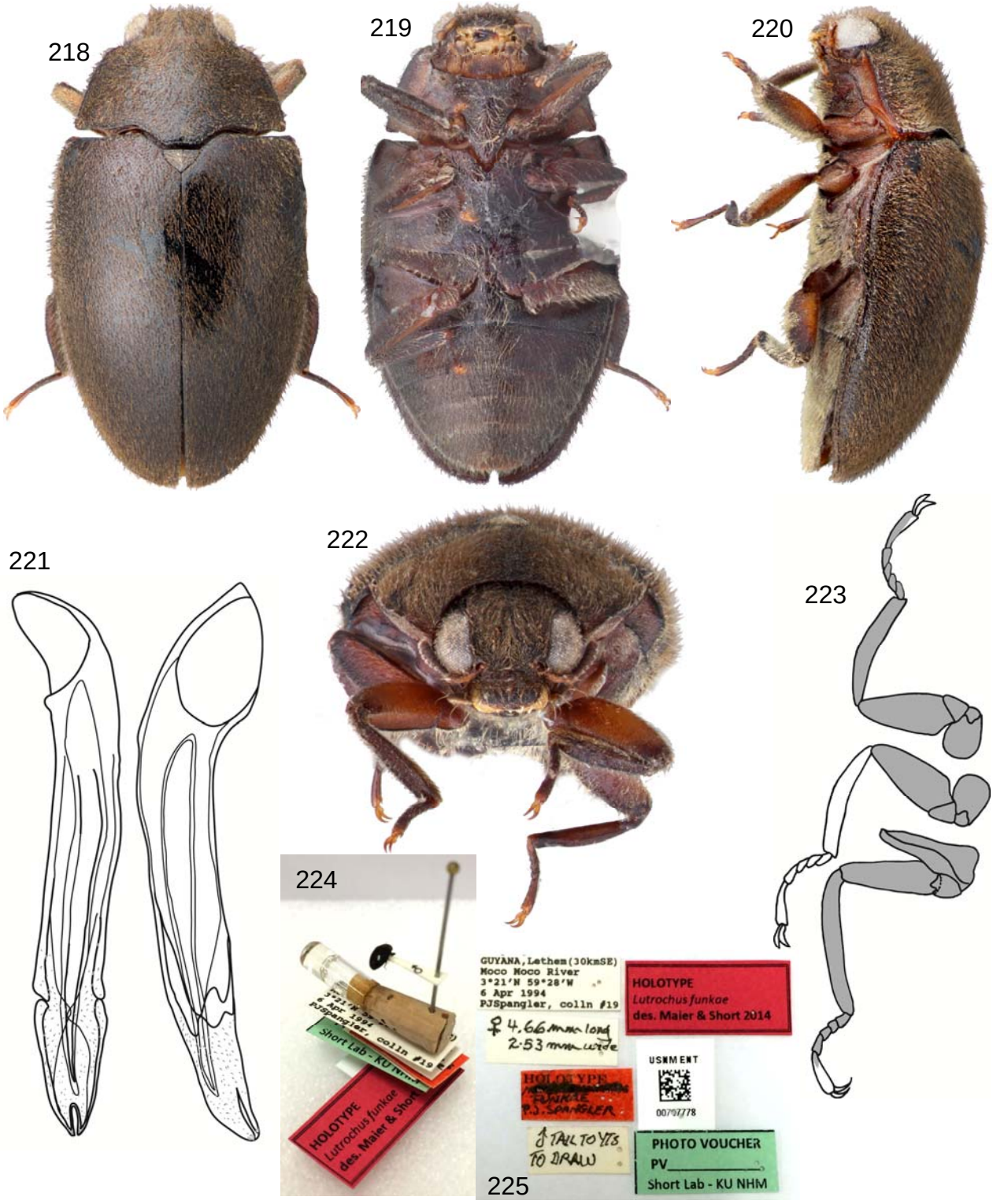


Lutrochus cauraensis Maier & Short, 2013 206. Dorsal habitus. 207. Ventral habitus. 208. Lateral Habitus. 209. Metatarsus, showing setation. 210. Metatibia, showing setation. 211. Protarsus, showing setation. 212. Setation of the dorsum, detail.

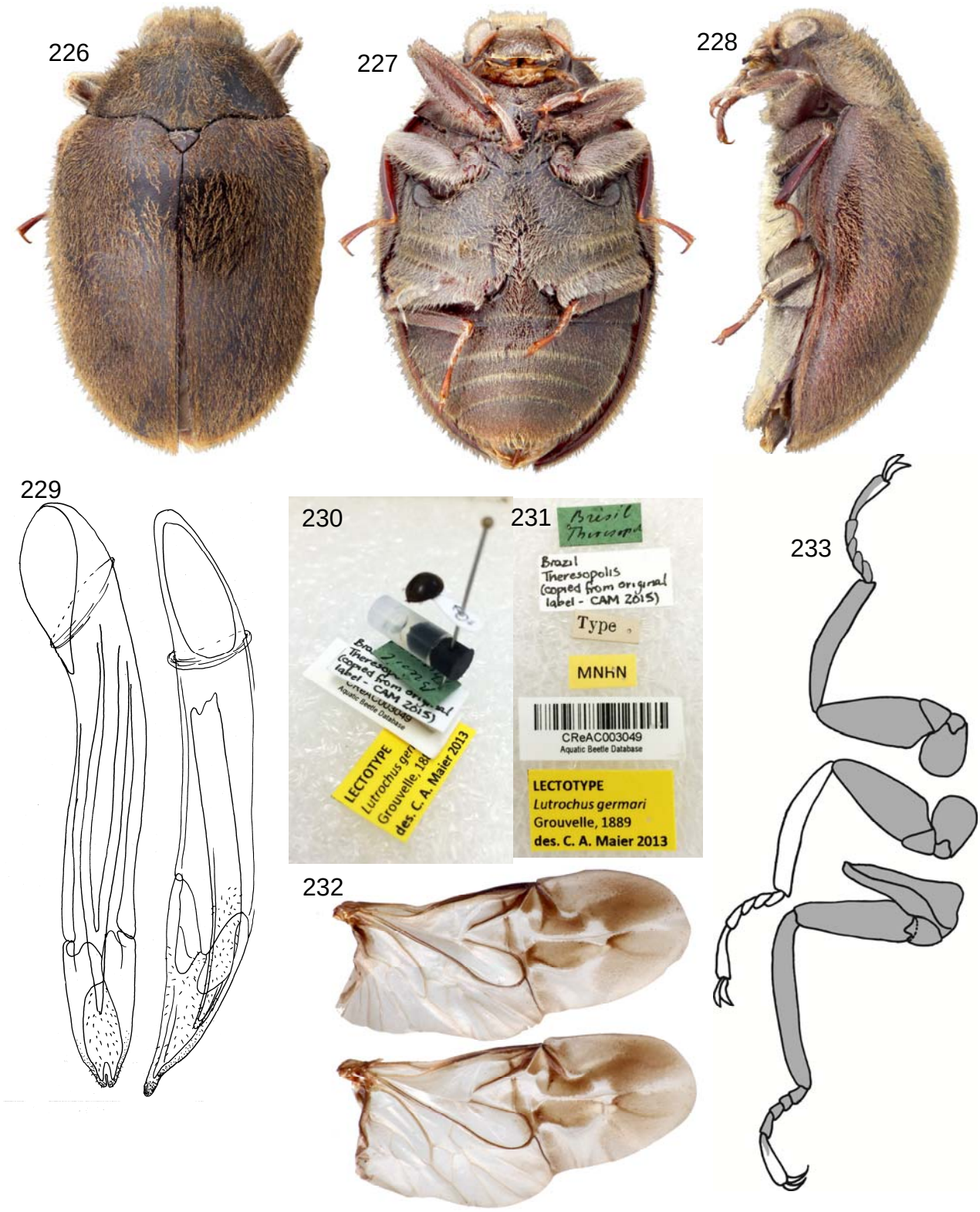




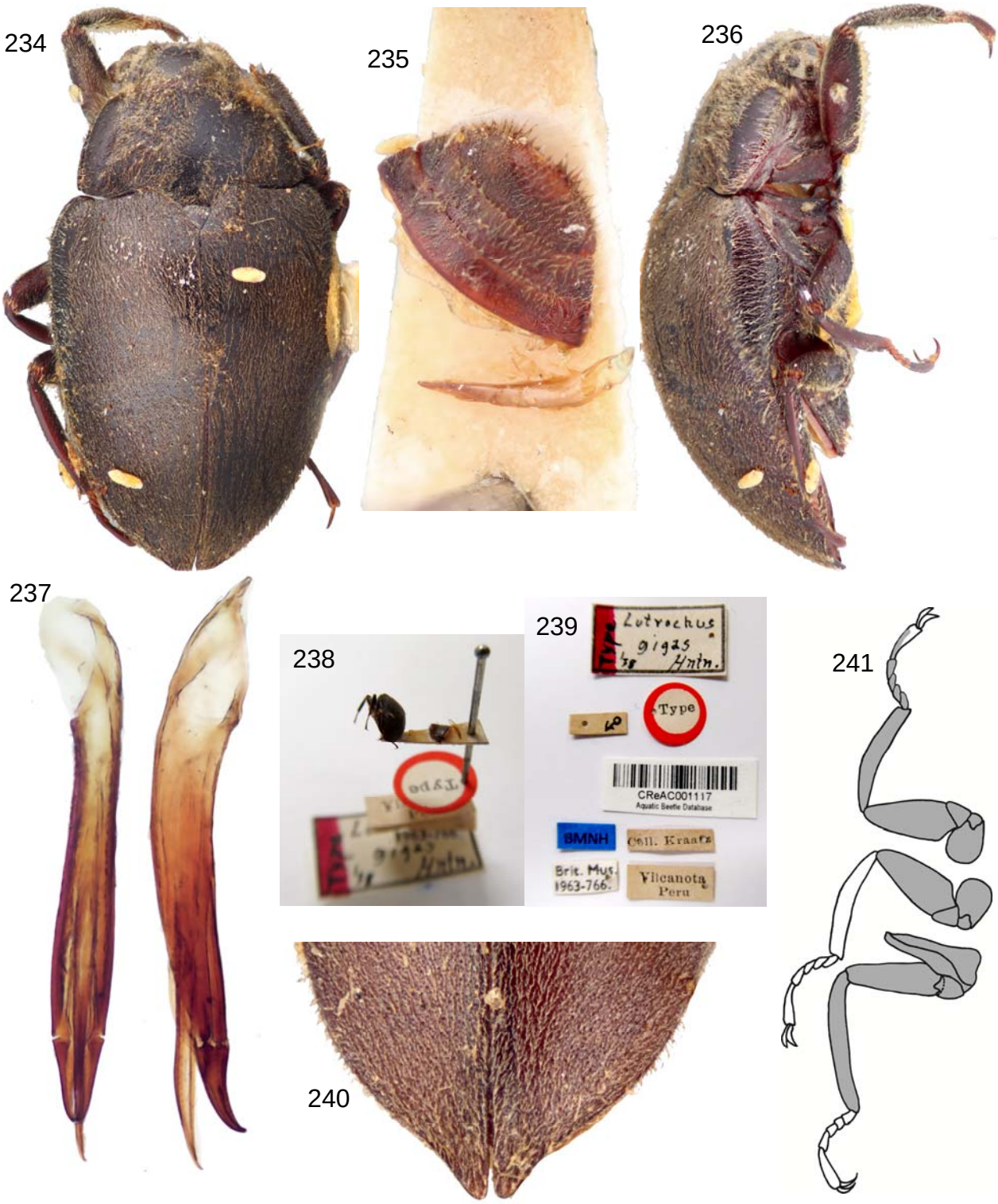
Lutrochus cauraensis Maier & Short, 2013 213. Dorsum, showing punctation. 214. Male genitalia, dorsal/lateral views. 215. Schematic representation of setation of legs. 216. Holotype specimen labels. 217. Holotype specimen, posterior view.



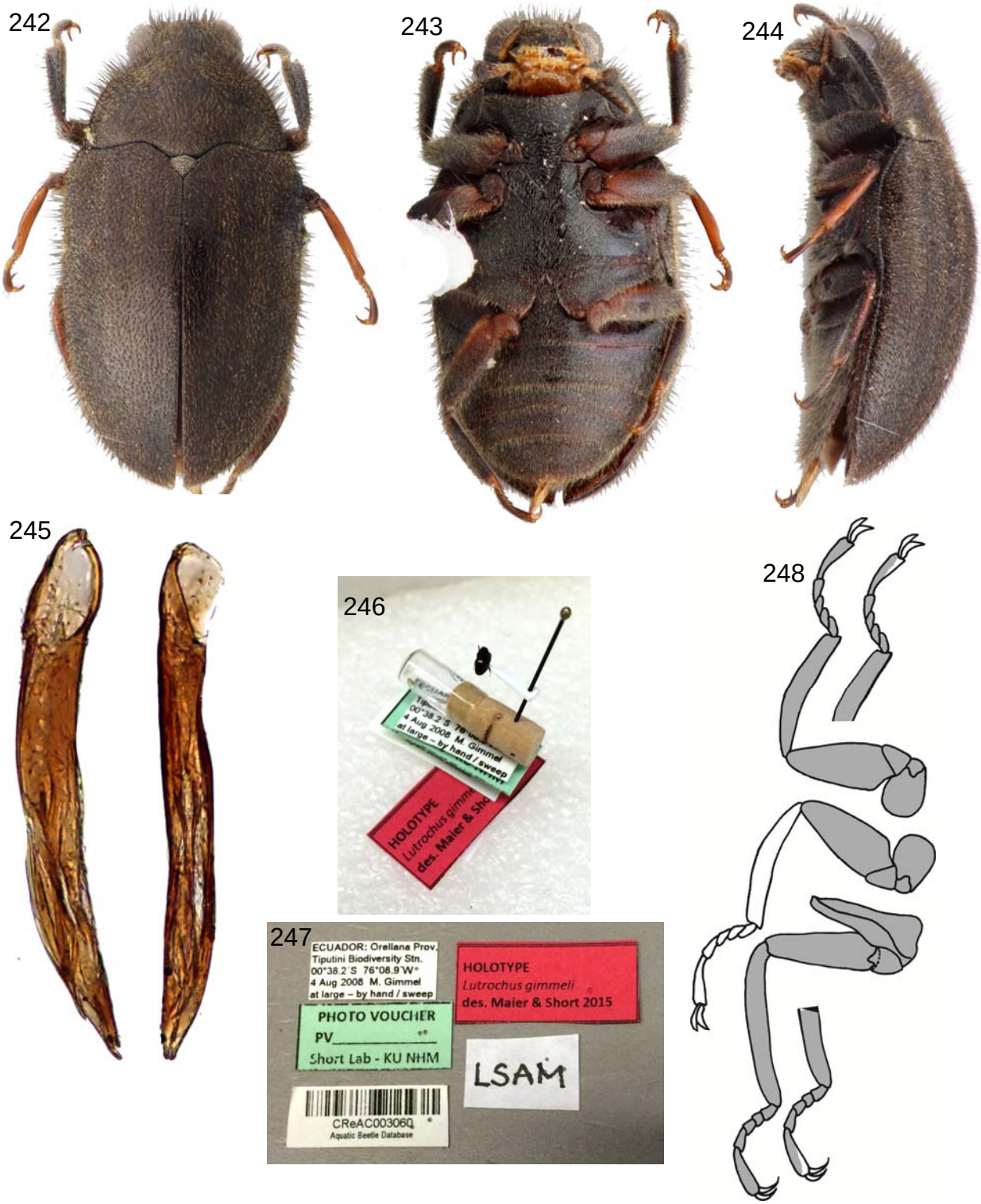
Lutrochus funkae Maier & Short 2014. 218. Dorsal habitus. 219. Ventral habitus. 220. Lateral Habitus. 221. Aedeagus, dorsal and lateral views. 222. Habitus, anterior view. 223. Schematic drawing of legs, showing setation pattern. 224. Holotype, on pin, posterior view. 225. Holotype labels.



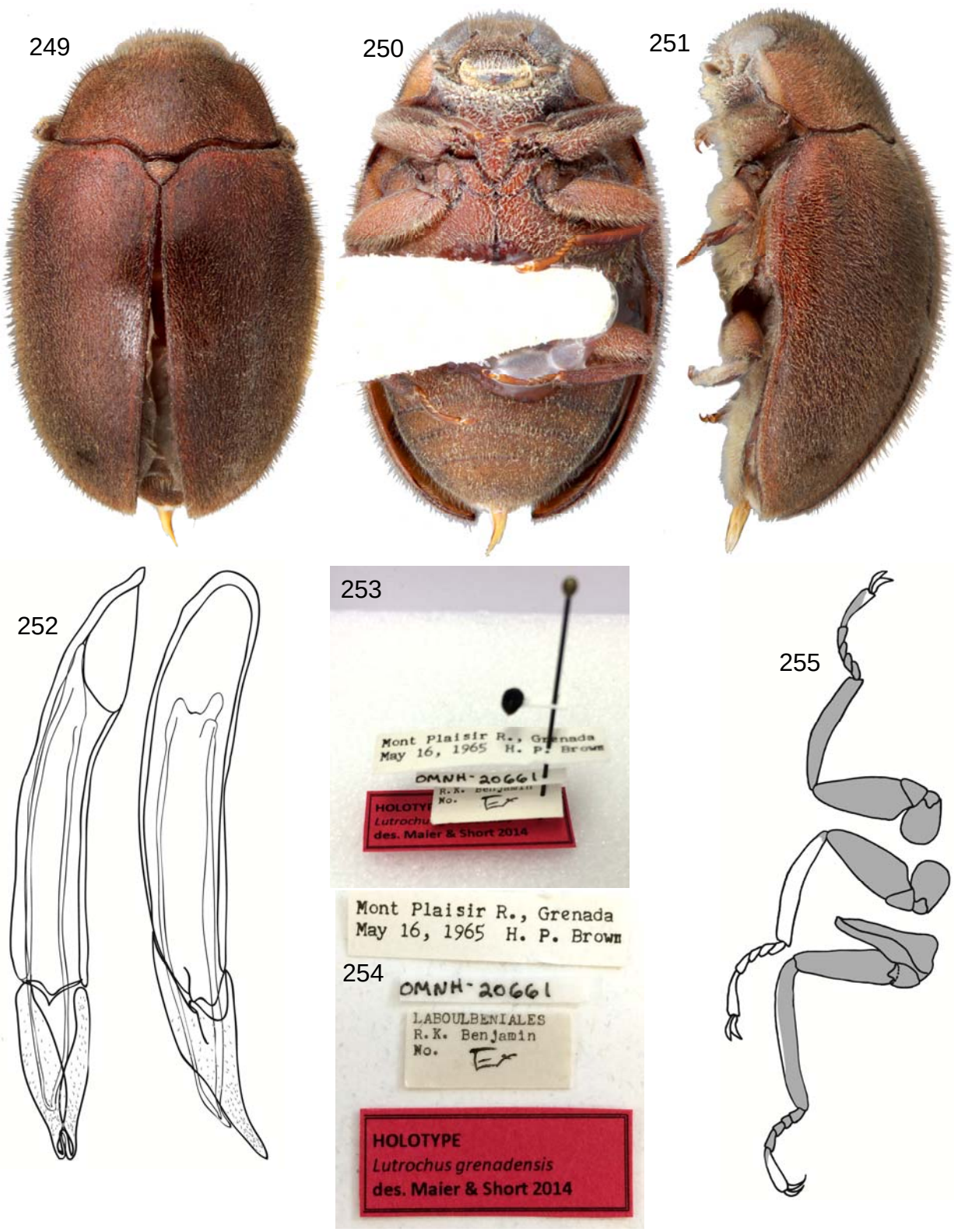
Lutrochus germari Grouvelle 226. Dorsal habitus. 227. Ventral habitus. 228. Lateral habitus. 229. Aedeagus, Dorsal/lateral views. 230. Holotype specimen, posterior view. 231. Holotype specimen labels. 232. Wing. 233. Schematic representation of setation of legs.



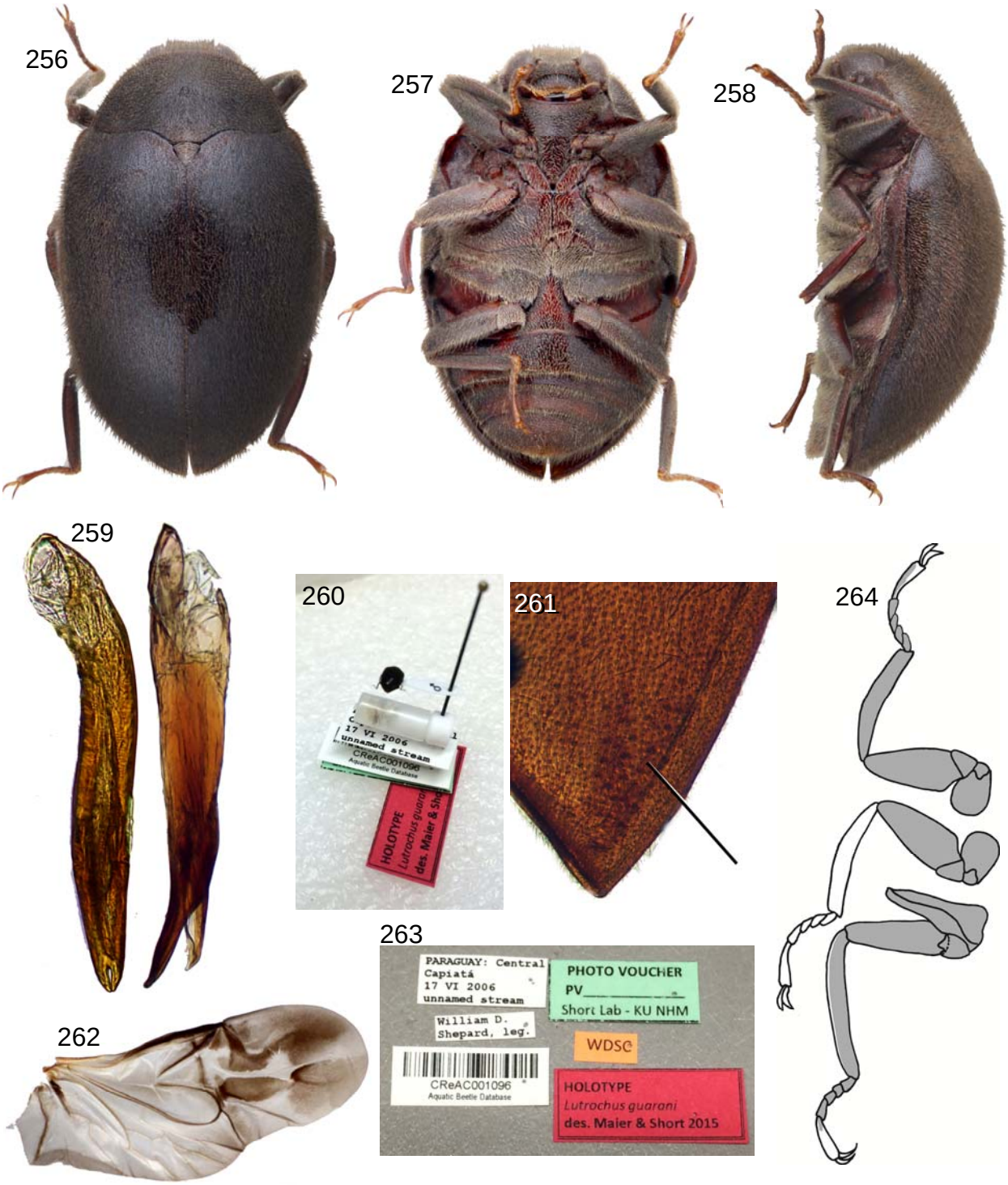
Lutrochus gigas Hinton 234. Dorsal habitus. 235. Abdominal apex & genitalia. 236. Lateral habitus. 237. Aedeagus, Dorsal/Lateral Views. 238. Holotype specimen, posterior view. 239. Holotype specimen labels. 240. Elytral apex. 241. Schematic representation of setation of legs.



Lutrochus gimmeli **n. sp.** 242. Dorsal habitus. 243. Ventral habitus. 244. Lateral Habitus. 245. Aedeagus, Dorsal/Lateral Views. 246. Holotype specimen, posterior view. 247. Holotype specimen labels. 248. Schematic representation of setation of legs - note, inset shows setation on internal face of tarsi.

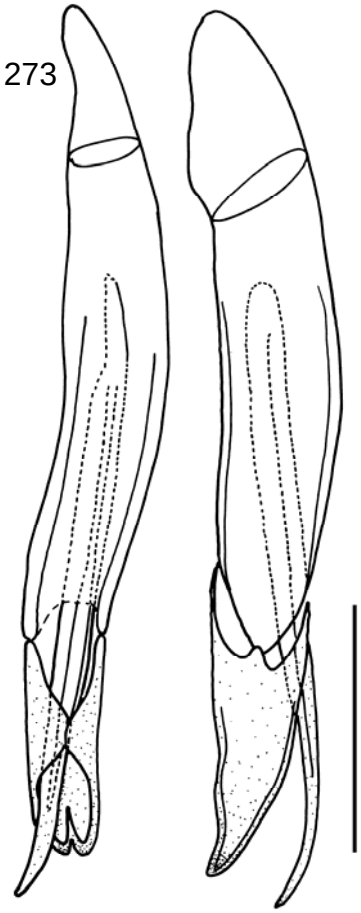


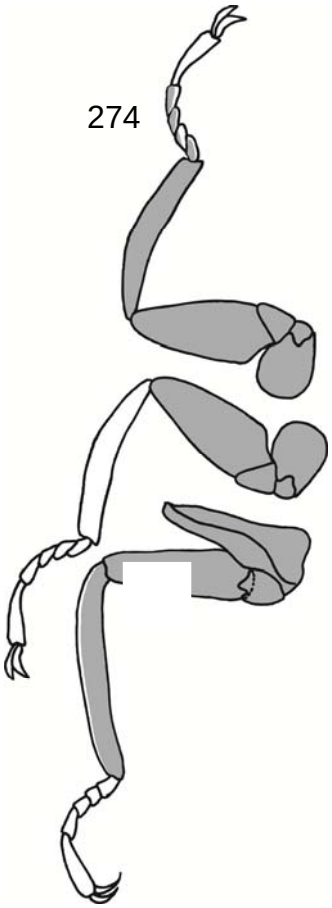
Lutrochus grenadensis Maier & Short 2014.249. Dorsal habitus. 250. Ventral habitus. 251. Lateral Habitus. 252. Aedeagus, dorsal and lateral views. 253. Holotype labels. 254. Holotype, on pin, posterior view. 255. Schematic drawing of legs, showing setation pattern.



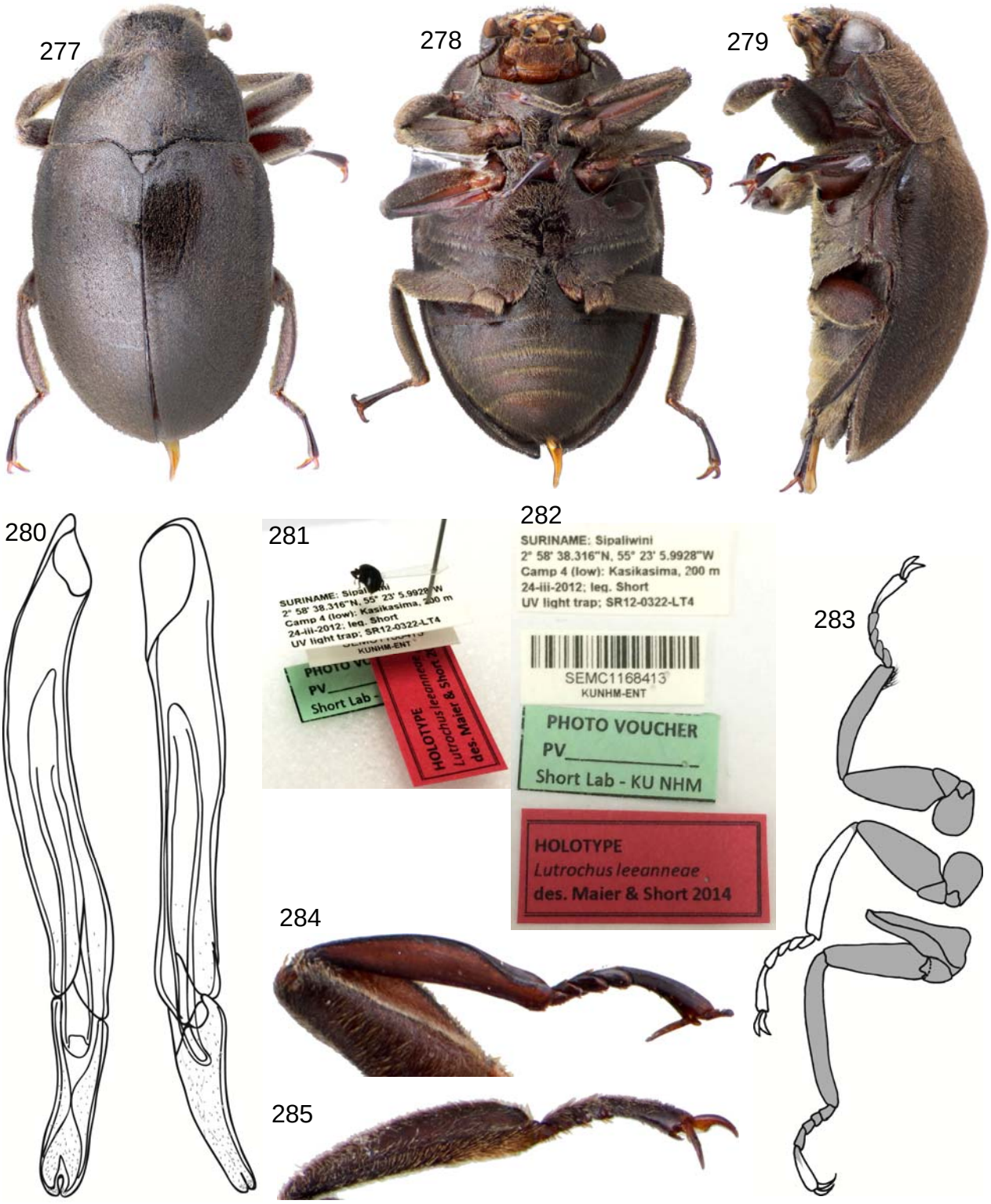
Lutrochus guarani **n. sp.** 256. Dorsal habitus. 257. Ventral habitus. 258. Lateral habitus. 259. Aedeagus, Dorsal/ Lateral Views. 260. Holotype specimen, posterior view. 261. Elytron, internal view, cleared specimen, showing "apical wing binding patch." 262. Wing. 263. Holotype specimen labels. 264. Schematic representation of setation of legs.

Lutrochus gustafsoni Maier & Short, 2013 265. Dorsal habitus. 266. Ventral habitus. 267. Lateral Habitus. 268. Elytra, detail, showing setation. 269. Protarsus, showing setation.

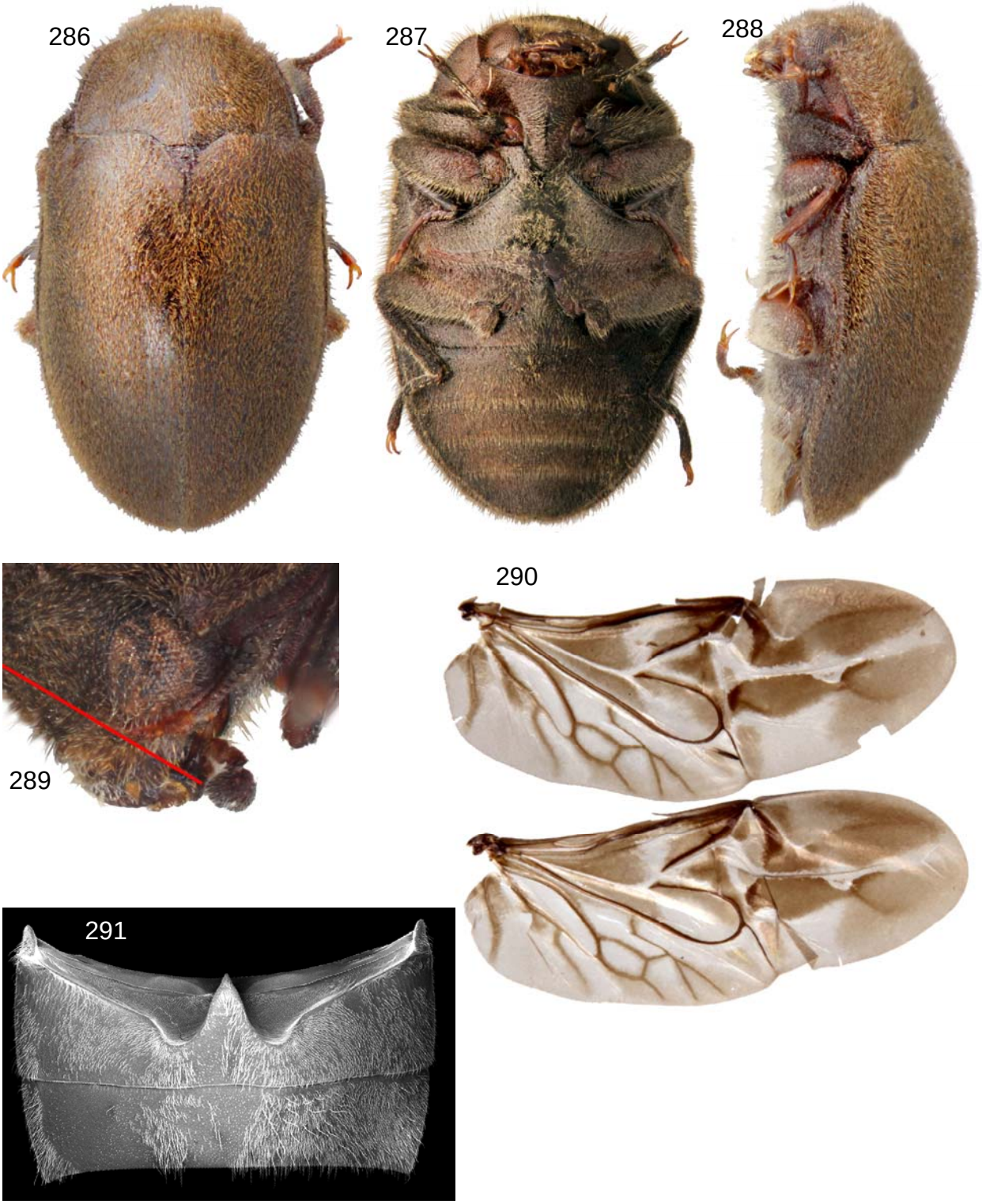




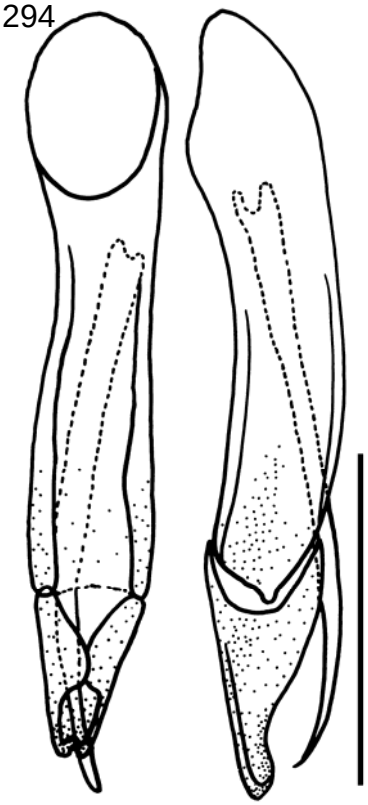
Lutrochus gustafsoni Maier & Short, 2013 270. Protibia, showing setation. 271. Meso-tibia and tarsus, showing excavation of mesotibia. 272. Metatarsus, showing setation. 273. Male genitalia, dorsal and lateral views. 274. Schematic representation of setation of legs. 275. Holotype specimen labels. 276. Holotype specimen, lateral view.

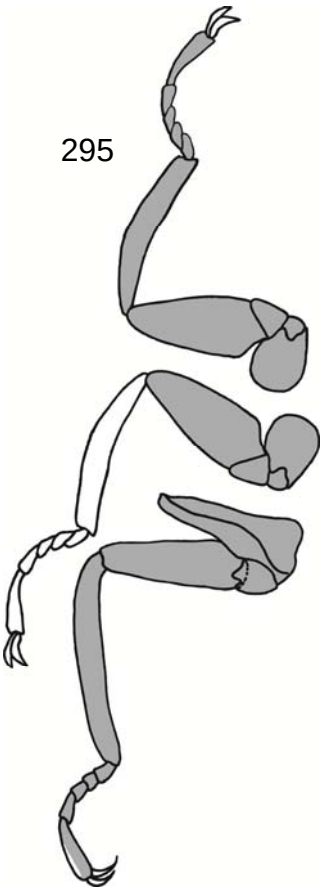


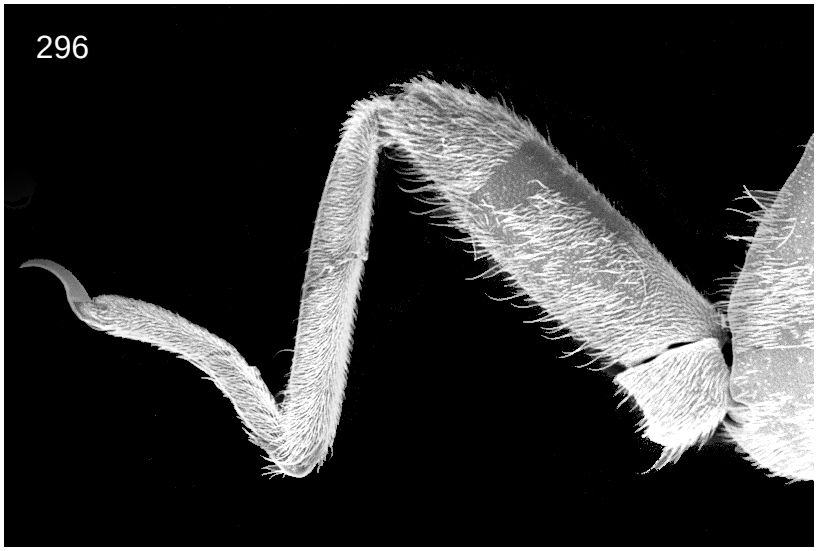
Lutrochus leeanneae Maier & Short 2014. 277. Dorsal habitus. 278. Ventral habitus. 279. Lateral Habitus. 280. Aedeagus, dorsal and lateral views. 281. Holotype, on pin, posterior view. 282. Holotype labels. 283. Schematic drawing of legs, showing setation pattern. 284. Mesoleg, showing lateral expansion of the mesotibia. 285. Proleg, showing lateral expansion of the protibia.



Lutrochus maldonadoi Maier & Short 2013. 286. Dorsal habitus. 287. Ventral habitus. 288. Lateral Habitus. 289. Head, oblique view, showing maxillary palps. 290. Wings, left and right. 291. First and second abdominal ventrites, SEM.







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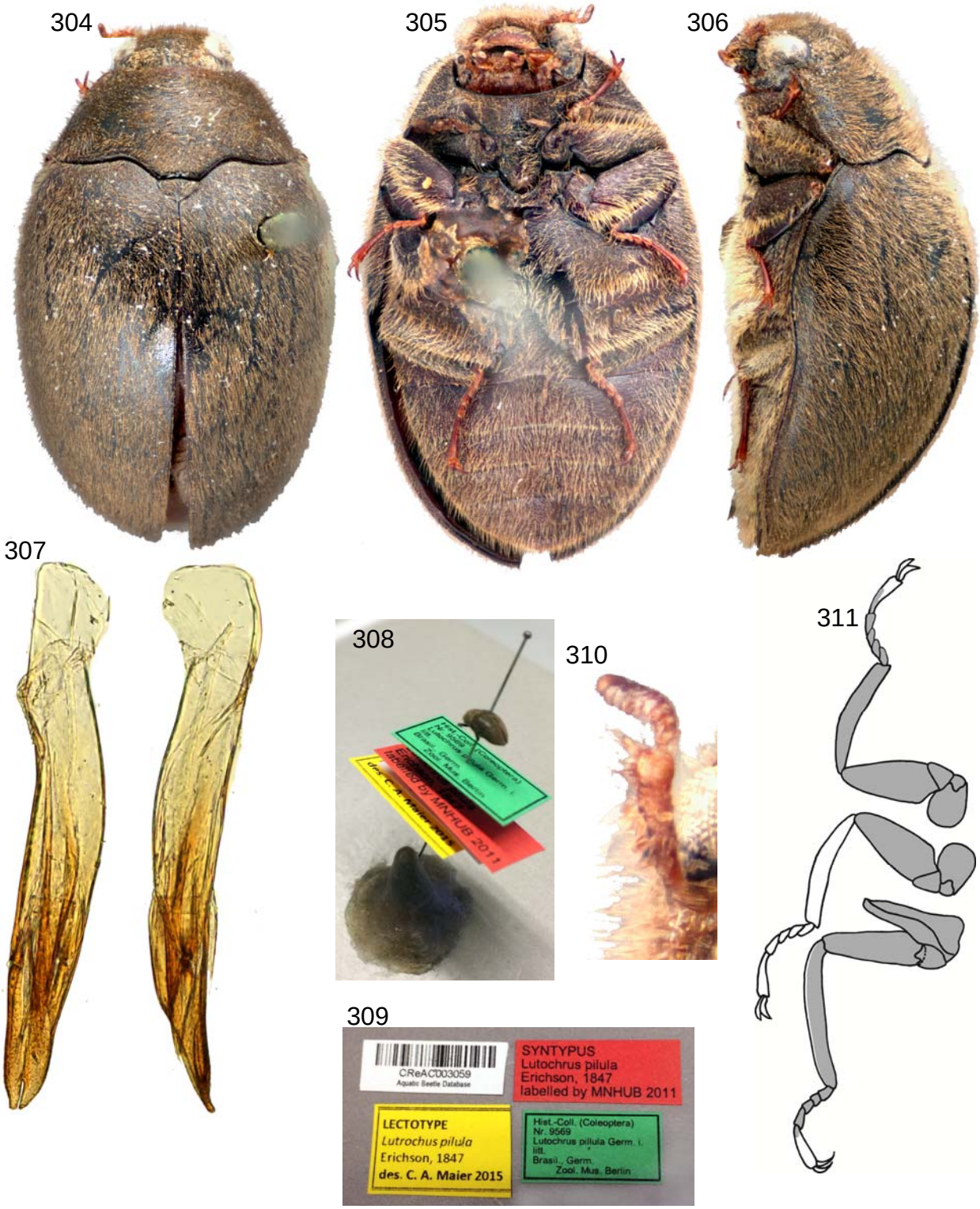
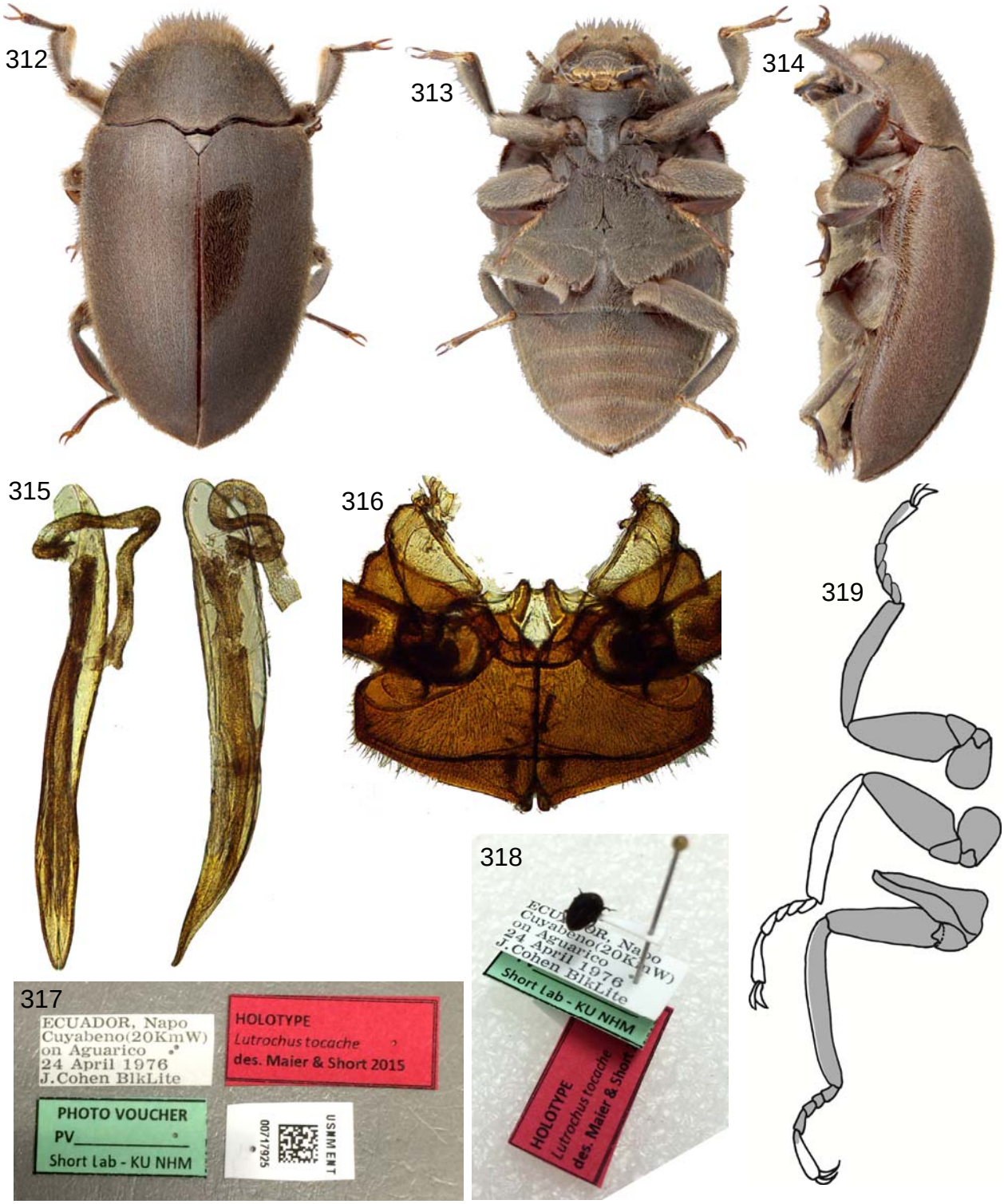
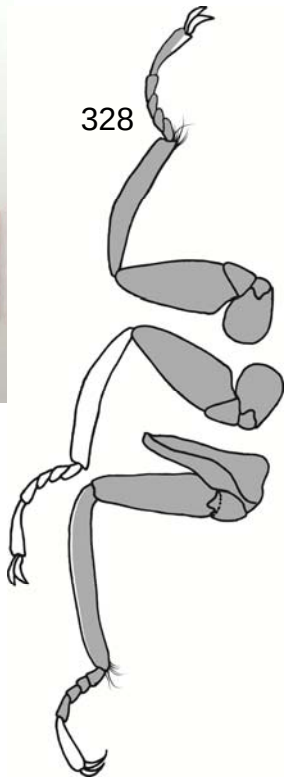


Lutrochus pilula Erichson 304. Dorsal habitus. 305. Ventral habitus. 306. Lateral habitus. 307. Aedeagus, Dorsal/Lateral Views. 308. Holotype specimen, posterior view. 309. Holotype specimen labels. 310. Antenna. 311. Schematic representation of setation of legs.



Lutrochus tocache Maier & Short 312. Dorsal habitus. 313. Ventral habitus. 314. Lateral Habitus. 315. Aedeagus, Dorsal/Lateral Views. 316. Meso– and Meta-ventrites. 317. Holotype specimen labels. 318. Holotype specimen, posterior view. 319. Schematic representation of setation of legs.



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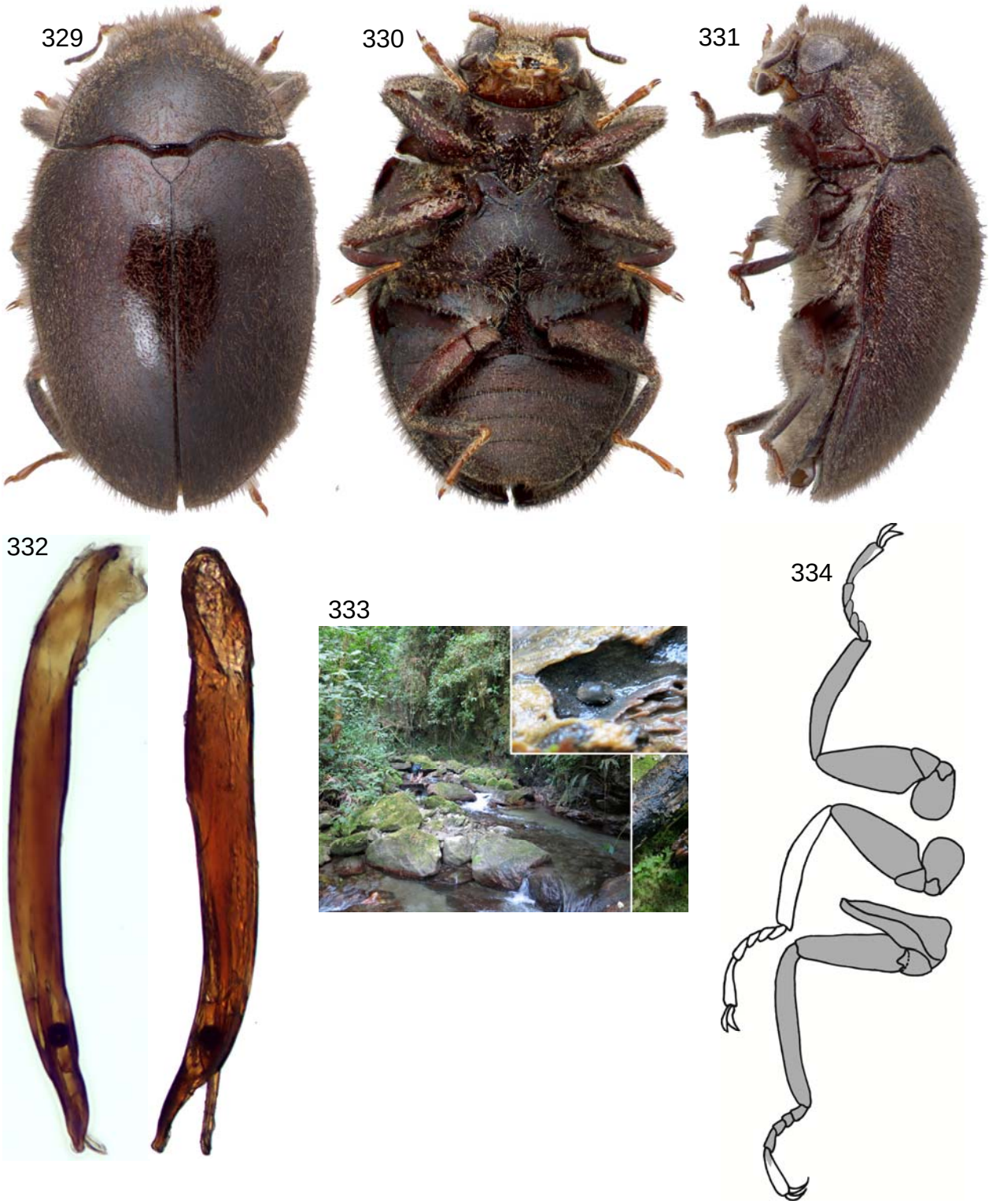

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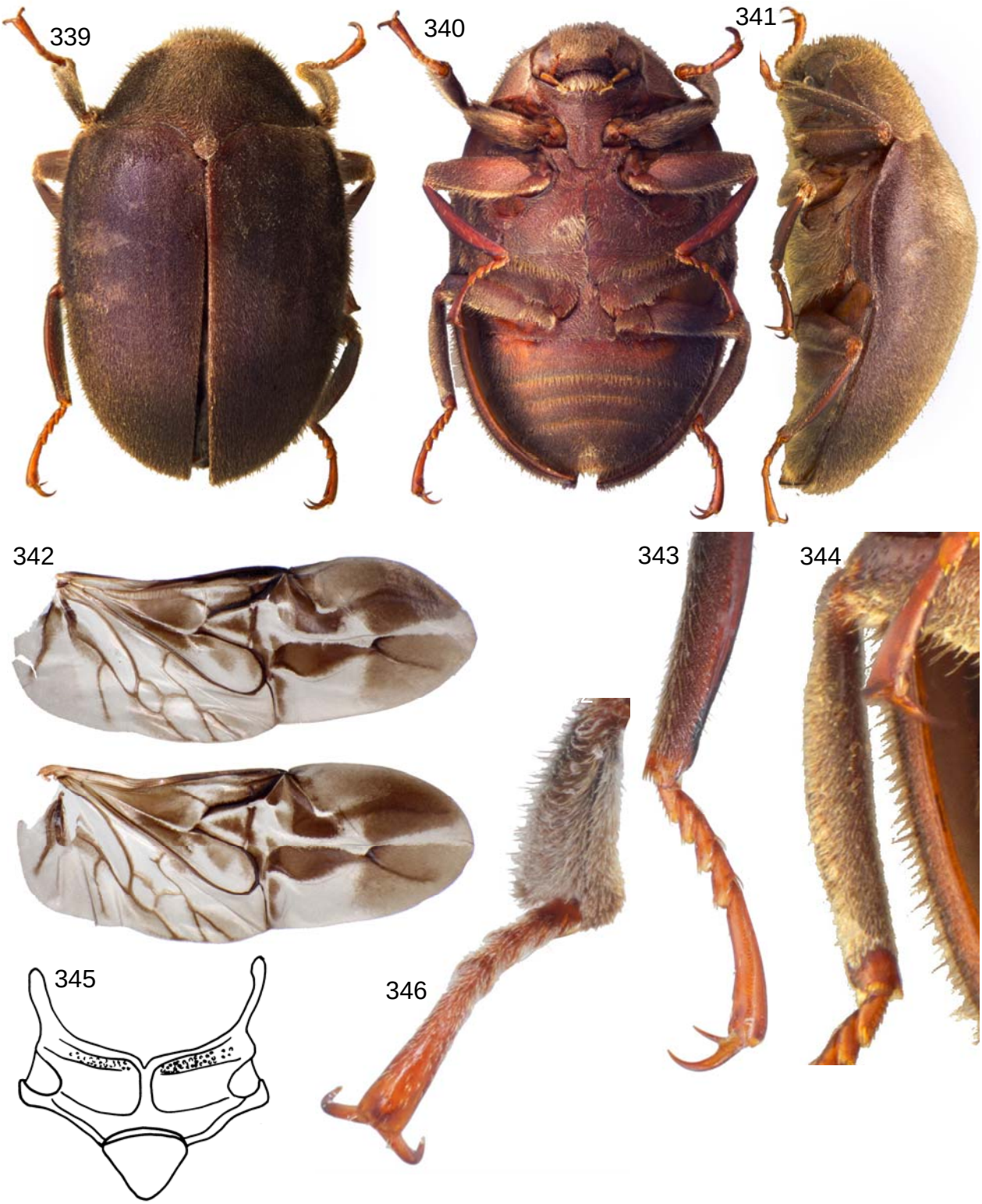
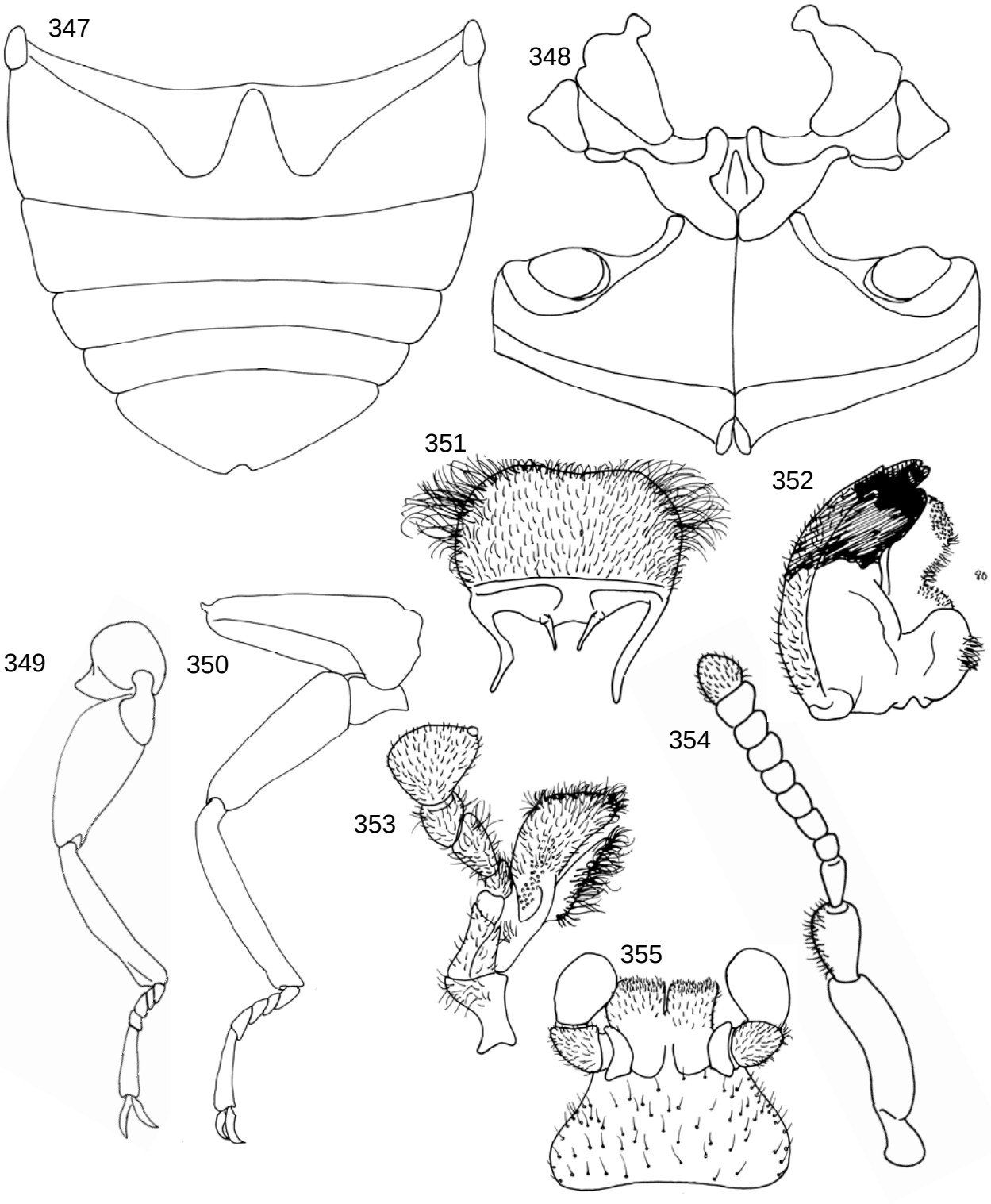
Lutrochus vestitus Sharp, 1882. 335. Holotype, dorsal view 336. Holotype, lateral view. 337. Holotype specimen, card mount. 338. Holotype specimen labels.



Lutrochus violaceus Maier & Short, 2013 339. Dorsal habitus. 340. Ventral habitus. 341. Lateral Habitus. 342. Wings, left and right. 343. Mesotarsus, showing setation. 344. Metatibia, showing setation. 345. Scutellum, cleared. 346. Protarsus, showing setation.



Lutrochus violaceus Maier & Short, 2013 347. Abdomen, male, ventral view. 348. Meso– and metaventrites. 349. Mesoleg. 350. Metaleg. 351. Mouthparts, Labrum. 352. Mouthparts, Mandible. 353. Mouthparts, Maxilla. 354. Antenna, showing representative setation on distal antennomere. 355. Mouthparts, Labium, showing representative setation on proximal palpomeres.

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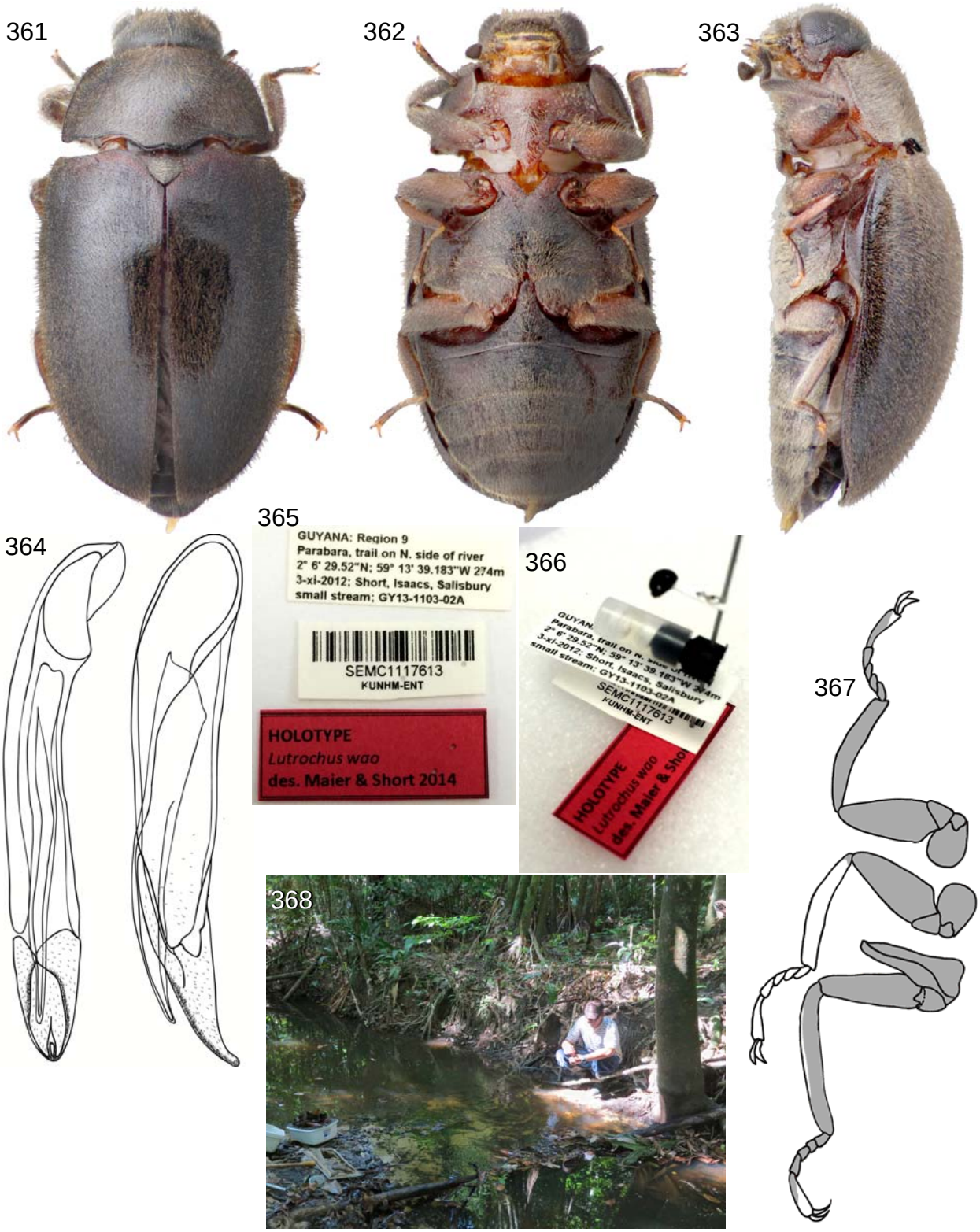
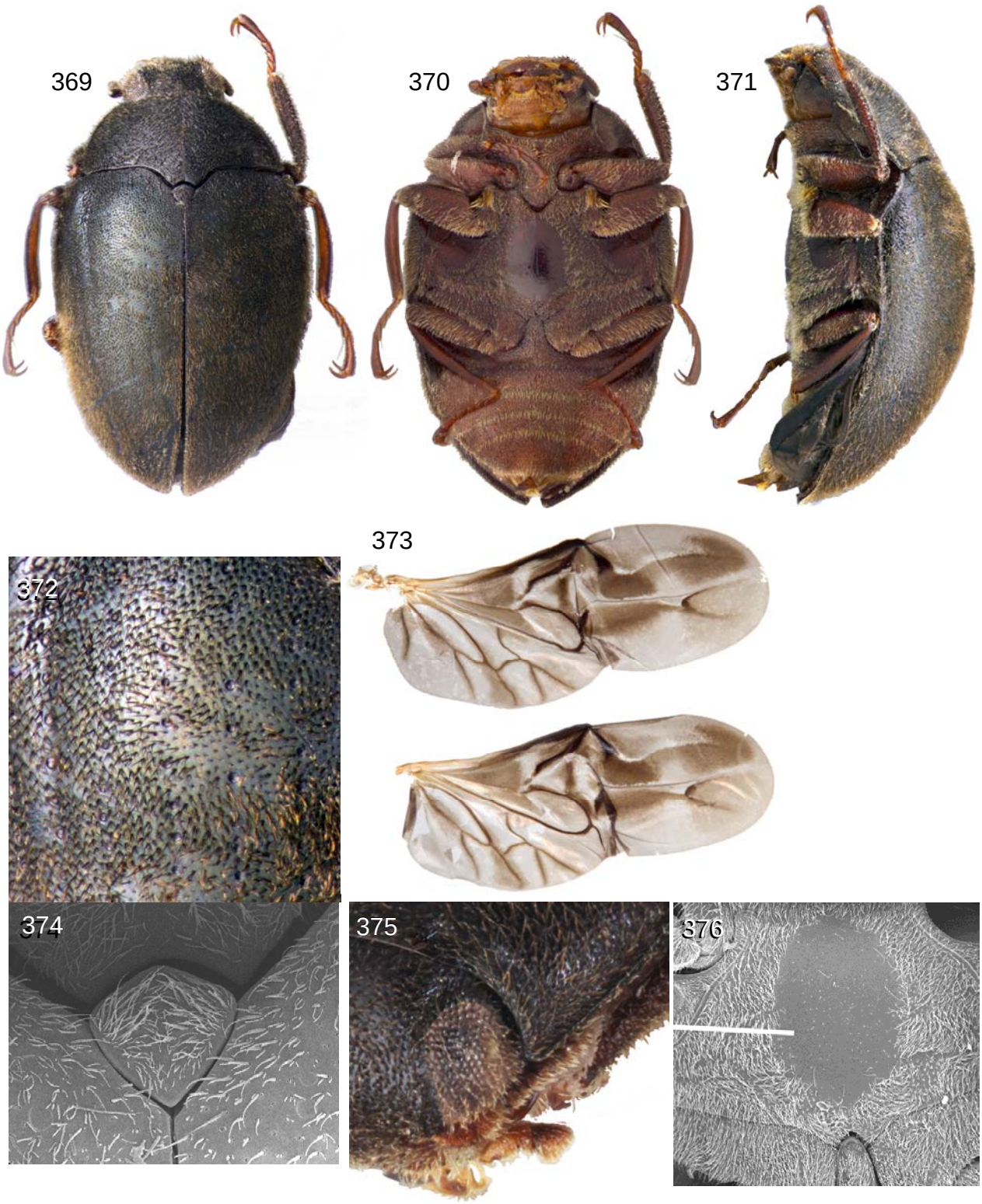
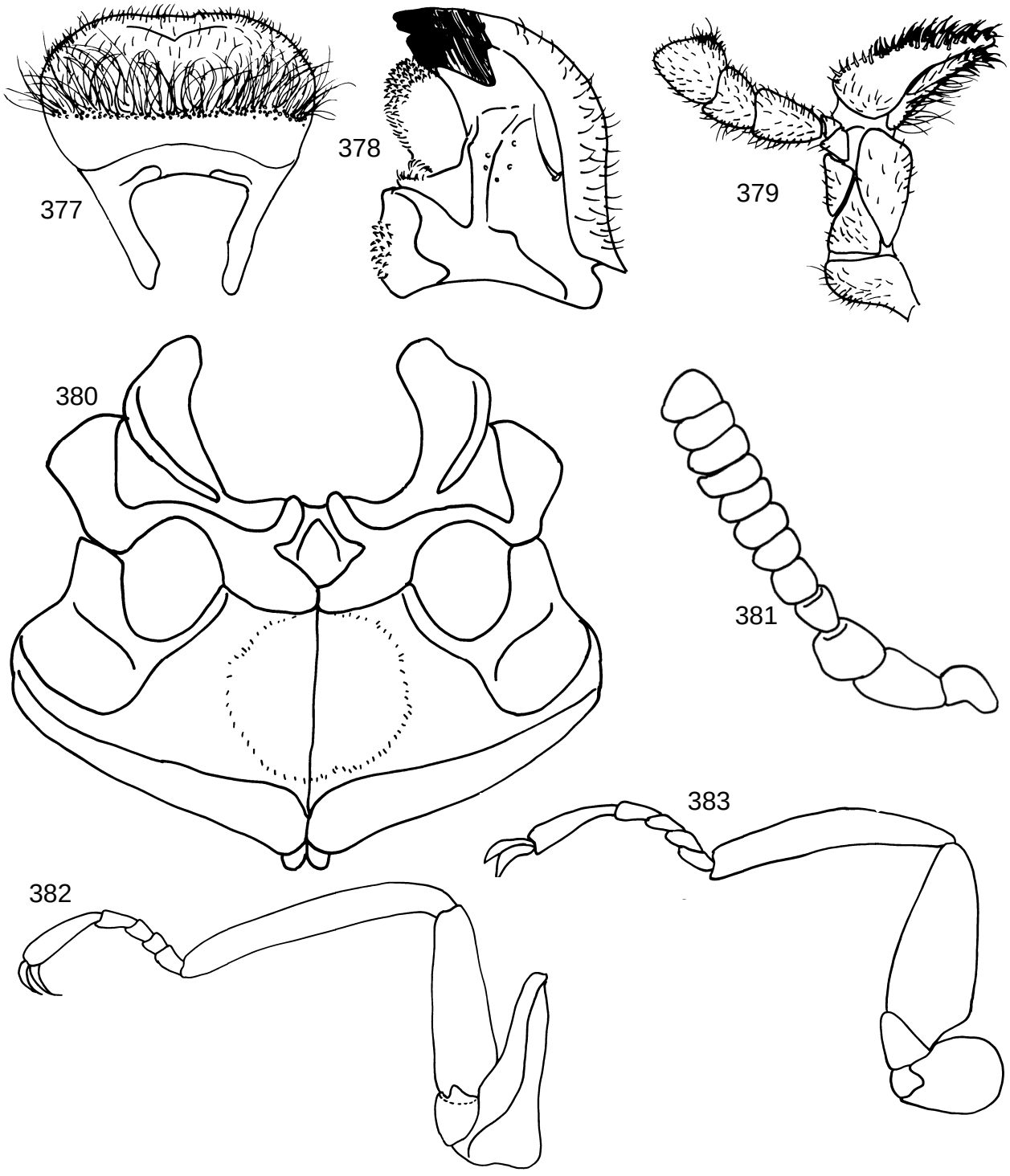


Lutrochus wao Maier & Short 2014. 361. Dorsal habitus. 362. Ventral habitus. 363. Lateral Habitus. 364. Aedeagus, dorsal and lateral views. 365. Holotype labels. 366. Holotype, on pin, posterior view. 367. Schematic drawing of legs, showing setation pattern. 368. Habitat of *L. wao*, in Parabara, Guyana.



Saxitrochus meridaensis (Maier & Short 2013) 369. Dorsal habitus. 370. Ventral habitus. 371. Lateral habitus. 372. Elytral punctation. 373. Hind wings, left and right. 374. Scutellum. 375. Head, oblique view. 376. Metaventrite, showing glabrous patch.



Saxitrochus meridaensis (Maier & Short 2013) 377. Mouthparts, labrum. 378. Mouthparts, mandible. 379. Mouthparts, maxilla. 380. Mesoventrite and metaventrite, cleared. 381. Antenna, showing representative setation on apical antennomere. 382. Metaleg. 383. Mesoleg.

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